BIOGEOGRAPHICAL AND ECOLOGICAL NOTES ON THE GENUS *TIKUNA* SAVAGE, FLOWERS, AND PORRAS (EPHEMEROPTERA: LEPTOPHLEBIIDAE) FROM CENTRAL AND SOUTH AMERICA[1]

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ABSTRACT: New records of *Tikuna atramentum* (Traver) (Leptophlebiidae) from Costa Rica show that this species can live in both temporary and permanent streams. All known localities are closely associated with Nicoya Complex terranes. Range maps are given for the other known species and an undescribed morphospecies of *Tikuna* and the biogeography of the genus is discussed.

KEY WORDS: *Tikuna,* Ephemeroptera, Leptophlebiidae, Nicoya Complex, temporary streams

Recently, Savage et al. (2005) described the genus *Tikuna,* containing the single species *T. atramentum* (Traver) from the Nicoya and Santa Rosa peninsulas of Costa Rica. Data at time of that publication indicated that this mayfly was a specialist in temporary streams closely associated with the Cretaceous geology of the Nicoya Complex. Since the publication of Savage et al. (2005), additional collecting in Costa Rica has substantially extended the known range of *T. atramentum,* and a second South American species, *Choroterpes bilineata* Needham and Murphy has been transferred to *Tikuna* (Peters et al. 2005). In this paper we report new localities for *T. atramentum*, give additional information about its biology, and discuss the biogeography of *Tikuna.*

Tikuna atramentum (Traver)

In addition to the localities in northwestern Costa Rica previously reported (Savage et al. 2005), we now have collected this species from the following localities:

COSTA RICA: Guanacaste; Nandayure, 11M subimagos, 5 F subimagos, 11 nymphs, Río Maquenco, 392 m, N 9°58.36' W 85°15.59', 16-II-2005, S. Ávila, R. W. Flowers, W. Porras; 30 nymphs, Parque Nacional Diriá, Quebrada Diriá, 162 m., N 10°11.41' W 85°35.94', 15-II-2005, S. Ávila, R. W. Flowers, W. Porras. Puntarenas; 17 nymphs, Peninsula de Osa, Parque Nacional Corcovado, Río San Pedrillo, N 8°37.90', W 83°43.546', S. Ávila, R. W. Flowers; Golfito, 1 M subimago (reared), 2 nymphs, Río Claro de Pavones (Peninsula Burica), Queb. Macho, 40 m, N 8°24.40' W 83°6.89', 16-IV-2005, S. Ávila; Quebrada Kilometer 20, 31 m., N 8°37.1', W 83°06.64', 1 nymph, 9-II-2005, S.Ávila, R. W. Flowers, G. Porras, 4 nymphs, 19-III-2005, S. Ávila. 1 nymph, Parrita, Quebrada Pirris, 7 km north of Parrita, 47 m., N 9°36.02', W 84°19.32', 13-II-2005, S. Ávila, R. W. Flowers.

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These new records (Fig. 1) extend the range of *T. atramentum* south along the Pacific coast of Costa Rica, and well beyond the dry forest habitats where it was first collected. In all cases the nymphs were found inhabiting leaf packs in pools or areas of quiet water. Water temperatures varied from 25° C to 28°C. In contrast to the localities in the Santa Elena and Nicoya peninsulas where the streams are dry for up to five months of the year (Savage et al. 2005), the streams in Burica and Osa are in one of the wettest areas of Costa Rica. The Parrita locality is in a transitional area between the northwestern dry forest and the much wetter Osa Peninsula. Apparently, *T. atramentum*, like *Ulmeritoides acosa* Ávila and Flowers (2005), can live in both temporary and permanent stream habitats.

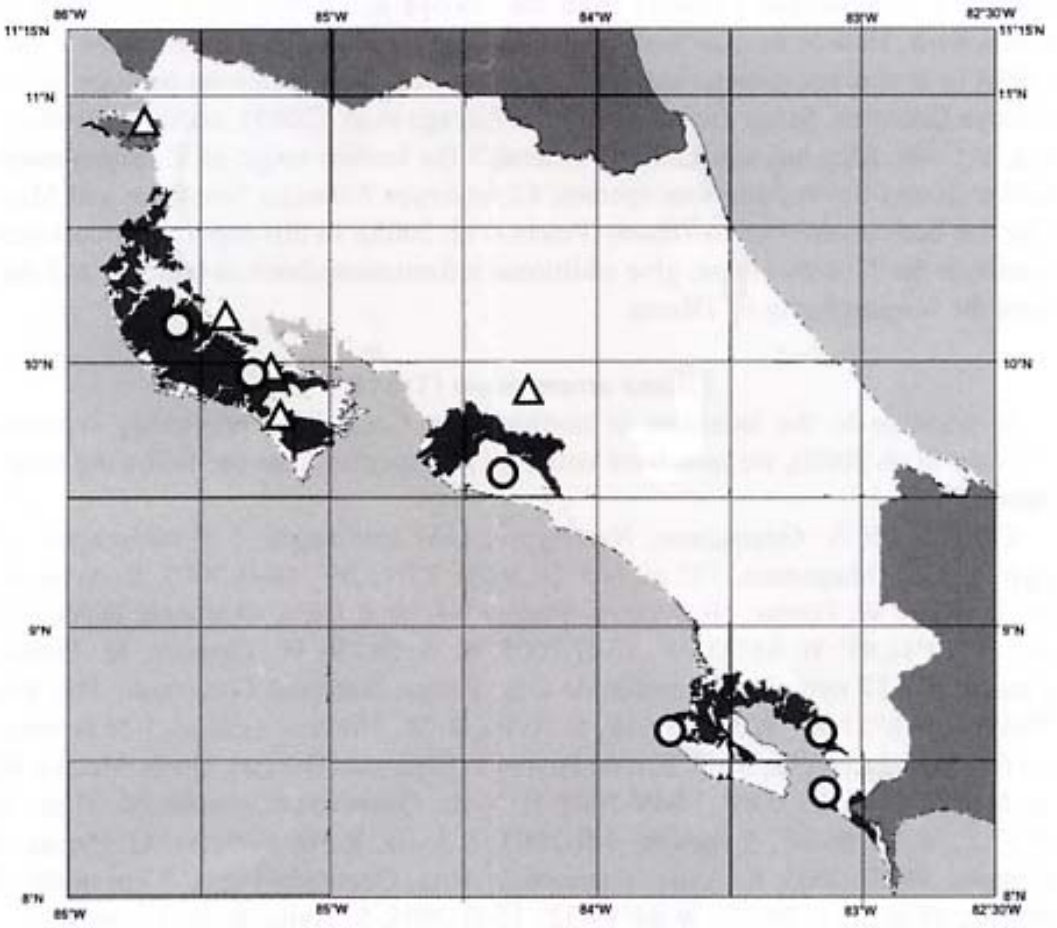

Fig. 1 Map of Costa Rica showing localities of *Tikuna atramentum*: circles, new records; triangles, records from Savage et al., 2005. Ophiolitic terranes are shown in dark grey.

Although the latest collecting records for *T. atramentum* have shown that this species is not limited to temporary streams, these localities give added weight to the association with Cretaceous geological formations. Figure 1 shows the known distribution of *Tikuna atramentum* in Costa Rica, both from this study and from Savage et al. (2005), along with the location of Cretaceous ophiolitic formations. The localities in Osa and Burica are on or very close to ophiolitic areas, and the Parrita locality is on a more recent terrane but close and downstream to an extensive Cretaceous terrane.

Tikuna bilineata (Needham and Murphy)

Figure 2 shows the distribution of *T. bilineata* based on the localities in Peters et al. (2005). The track was drawn using the method of Morrone (2004). *Tikuna bilineata* is a widespread, but rarely collected Amazon basin species. All known specimens are imagos or subimagos (Peters et al., 2005) and nothing is known of the nymphal morphology or its habitats.

Tikuna undescribed species

Savage (1983) discussed a species of *Tikuna* known from both the north coast of Panamá and western Ecuador (Fig. 2), but this species is known only from a few subimagos and has not been formally described.

DISCUSSION

Tikuna shows a vicariant distribution pattern common to many trans-Andean plants and animals (Croizat 1958, 1976; Cracraft and Prum 1988): a widespread western Amazonian ancestral population separated from related taxa along the western coast of northwestern South America. The distribution of *T. atramentum* and *Tikuna* undescribed species west of the Andes could be attributed to either dispersal northward into the developing Lower Central America, or to additional tectonic events along the western edge of South America. We prefer the second explanation for several reasons.

First, there is no direct evidence of dispersal in any particular direction. Differentiation of these species from a widespread ancestor before the Tertiary uplift of the Andes is congruent with other vicariant patterns being found in different organisms such as birds and frogs (Croizat 1958, 1976, Kattan et al., 2004).

Second, the close geographic association of *T. atramentum* with ophiolitic terranes was noted in Savage et al. (2005), but the localities where the species was known at that time were all in highly seasonal streams that happened to be on ophiolitic terranes; present-day climate was just as likely as past geology to explain the distribution of the species. Our recent collecting now shows that *T. atramentum* is not limited to temporary streams, and the new records suggest

an even tighter spatial correlation with ophiolitic terranes. Recent studies on the biogeography of New Guinea have noted a similar close association of genera of aquatic Hemiptera (Polhemus and Polhemus 1998), plants, and birds of paradise (Heads 2002) with ophiolitic terranes. These taxa may have arrived in New Guinea by accretion of the terranes on which they occur. A similar accretion process may be responsible for the distribution of *T. atramentum* in Costa Rica.

Fig. 2. Distribution of known forms of *Tikuna*. Solid squares and lines, *T. bilineata*; circles and dashed line, *Tikuna* new species; heavy black line, *T. atramentum*.

Savage (1986) placed *Tikuna* (as "New Genus"), along with *Fittkaulus* and *Terpides,* in a group of Atalophlebiinae which separated very early—in the late Cretaceous or early Tertiary—from the main lineages of the Leptophlebiidae. If this hypothesis is correct, the mid Tertiary uplift of the northern Andes is sufficient to explain the separation of an ancestral stock into *T. bilineatea* east of the Andes and the two forms west of the cordillera.

Tectonic events along the western edge of South America can account for the separation of *T. atramentum* from the continental species (Fig. 2). Dispersal in the Pliocene–Pleistocene is traditionally invoked to explain most of the biodiversity of Costa Rica and Panamá, and it has generally been assumed that previous to this time there was a wide seaway separating the continents for around 60 million years. However, Briggs (1994) and Heads (2005) have cited evidence that some mollusk groups on the Atlantic and Pacific sides of Central America have been separated for much longer than the Pliocene–Pleistocene uplift. Meschede and Frisch (1998) give a detailed theory for an origin of the Costa Rica–Panamá arc close to South America that takes into account the objections to the long separation of North and South America in the Tertiary, and explains disjunct distributions like those of *Tikuna,* and botanical puzzles such as the close relationship between the flora of Osa with the Chocó (Wallace 1997).

Although research on tropical aquatic insects has traditionally focused on mountainous areas, *Tikuna* is an example of the still largely unknown Ephemeroptera fauna to be found in lowlands, temporary streams, and non-riffle habitats. More attention to these areas will give new insights into the biogeography of Neotropical aquatic ecosystems.

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