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Rediscovery of *Choroterpes atramentum* in Costa Rica, type species of *Tikuna* new genus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae), and its role in the "Great American Interchange"

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Abstract

A new genus, *Tikuna,* is described based on recent collections of adults and nymphs of *Choroterpes atramentum* Traver from western Costa Rica. All recent collections are from streams on or near the Nicoya Complex, the oldest geological formation in Lower Central America. *Tikuna* belongs to a lineage of South American Atalophlebiinae (Leptophlebiidae: Ephemeroptera) whose origin is hypothesized to have been in the late Cretaceous–early Tertiary. Some implications of the distribution of *Tikuna* for theories on the origin of Costa Rica's biota are discussed.

Key words: *Tikuna atramentum,* Ephemeroptera, Nicoya Complex, Lower Central America, new genus, plate tectonics

Resumen

Se describe un género nuevo, *Tikuna atramentum* (Traver) basado en colecciones recientes de adultos y ninfas del oeste de Costa Rica. Todos los registros recientes son de quebradas en o cerca del Complejo de Nicoya, la formación geológica más vieja en América Central Baja. *Tikuna* pertence a un linaje de Atalophlebiinae (Ephemeroptera: Leptophlebiidae) del América del Sur. Se plantea como hipótesis que el órigen de este linaje fuera tarde en el Cretácico hasta temprano en el Terceriario. Se discute algunas implicaciones que tiene la distribución de *Tikuna* para las teorías sobre el órigen de la biota de Costa Rica.

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Introduction

Traver (1947) described *Choroterpes atramentum* (Ephemeroptera: Leptophlebiidae) based on two male subimagos and a female imago from a group of mayflies collected in 1939 from the Río Pedregoso in Costa Rica. This species has for many years been an enigma because, while it has distinctive markings and is thus easy to recognize, no further specimens have been collected until recently. Savage (1983) studied Traver's specimens and concluded that *C. atramentum* was not related to *Choroterpes* but was an undescribed genus in the *Terpides* lineage, a group that currently consists of *Terpides* Demoulin, found in Central and Northern South America, and *Fittkaulus* Savage and Peters, currently known only from northern Brazil and the Guianas (Savage 1986).

In April 2002, additional male and female subimagos were found in a light trap sample from the Nicoya Peninsula near the town of Carmona. This was the first time in over 60 years that this species had been seen and recognized. During 2002, the two junior authors made two expeditions into the central and southeast areas of Nicoya and collected additional specimens including male and female imagos and small nymphs. In August 2002, additional adults were found in Malaise trap sample from the Santa Elena Peninsula in the extreme northwestern part of Costa Rica. In December, nymphs from Santa Elena were found in the Río Cuajiniquil, near where the Malaise traps had been sited.

With all life cycle stages and some of the biology now known, earlier conclusions that this species belongs to a new genus in the *Terpides* lineage are shown to be correct. We describe this new genus below. Methods, characters, and terminology used in this paper follow Savage and Peters (1983). Wing venational terminology follows Edmunds and Traver (1954). Additional discussion of characters may be found in Pescador and Peters (1980), Towns and Peters (1980) and Tsui and Peters (1975). Abbreviations for collections in which specimens are deposited are as follows: FAMU, Florida A&M University; INBio, Instituto Nacional de Biodiversidad; UCR, Universidad de Costa Rica.

Tikuna new genus (Figs. 1–25)

Type species. *Choroterpes atramentum* Traver 1947:156, here designated.

Imago: male eyes (Fig. 3): upper portions on very short, wide stalk; upper portions contiguous on meson of head; dorsally upper portions circular with small square, facets, facet color yellowish tan; from lateral view, maximum length of lower portions 0.7 maximum length of upper portions; facets of lower portions small, hexagonal, black. Female eyes (Fig. 4): separated on meson of head by a distance 2.5 times maximum width of an eye; margins of head and eyes posterolaterally extended: facets small, hexagonal, black. Ocelli with basal portion dark, apical portion light; lateral ocelli enlarged. Wing size: maximum width of forewings 3/10 maximum length of forewings; maximum length of hind wings 1/8 maximum length of forewings; maximum width of hind wings 0.54 maximum length of hind wings. Forewing (Fig. 1, 5); vein Rs forked 1/5 distance from base of vein to margin; vein MA forked approximately 1/2 distance from base of vein to margin, stem of MA sagged so MA fork often slightly asymmetrical, vein MP forked asymmetrically or MP_2 attached MP_1 by crossveins; ICu_1 attached at base to CuA; crossveins moderately numerous; stigmatic crossveins not anastomosed, marginal intercalaries along posterior margin. Hind wing (Fig. 2, 6): costal projection developed with apex truncate, apex located 3/4 distance from base to apex of wings, base of projection wide; length of vein Sc 4/5 length of wings; apex of wings acute, rounded; crossveins as in Fig. 2. Legs: all long, length 3/4 length of forewings; ratio of segments of male foreleg: 0.70: 1.00: 0.03: 0.38: 0.39: 0.23: 0.08; claws of a pair similar, with apical hook and opposing lobe (Fig. 10). Abdominal terga 8–9: large and acute posterolateral spines on tergum 9, small rounded posterolateral projections on tergum 8. Styliger (Fig. 11, 13): maximum length 1/3 maximum width; posteromedian margin gently rounded, posterolateral margins developed. Forceps: segment 3 1/2 length of segment 2: segment 2 slightly less than 1/10 length of segment 1; segment 1 with base wider, inner margin of base shaped as in Fig. 11, inner margin with long, narrow, pointed spines basally and very small rectangular, rounded spins apically; segments 2 and 3 shaped as in Fig. 11, segment 2 with very small rectangular spines on inner margin. Penes (Fig. 12): short, a little less than 1/2 length of forceps segment 1; basal 1/2 fused, apical 1/2 unfused, mid-lateral margins with projections, apices without appendages. Sternum 7 of female (Fig. 9) with broadly rounded genital extension. Sternum 9 of female (Fig. 9) with large posteromedian indentation and pointed submedian projections. Caudal filaments 1 1/2 to 2 times length of body; cerci and terminal filament subequal in length.

Nymph (Fig. 14) (in alcohol). Body length 6.1–7.5 mm. Head hypognathous, antennae 3 times maximum length of head. Clypeus with lateral margins straight, tapered apically, anteromedian margin straight to slightly convex. Labrum (Fig. 19): maximum width approximately equal to width of distal portion of clypeus; dorsum with apical setae, venter with setae submedially and laterally. Mandible: outer margin of left mandible (Fig. 20) relatively straight, outer margin of right mandible broadly curved; outer incisors with 4 teeth, inner incisors with 2 teeth; outer incisor of right mandible broad with 3 apical teeth and 1 tooth on inner lateral margin, and prostheca as in Fig. 20. Hypopharynx (Fig. 22): lingua lacking lateral processes, lingua widened distally with broad, median indentation; superlinguae with apical setae. Maxilla (Fig. 21): galea-lacinia with an inner subapical row of 6 pectinate setae, inner apical margin with 1 large pectinate seta and 1 large non-pectinate apically curved seta. Inner lateral margin with a row of long setae and a recessed row of 10 setae near apical margin, apical seta of recessed row larger, thick; segments 1–3 of palpi subequal; setae as in Fig. 21. Labium (Fig. 23): segment 3 conical with spine-like setae on inner margin, dorsum with a diagonal row of large setae medially, venter with narrow hair-like setae on outer margin and on ventral surface; segment 2 with hair-like setae on outer margin and on inner apical margin; segment 1 shaped as in Fig. 23, with setae on inner and outer margins, setae on outer margin thicker; paraglossae and glossae with dense setae as in Fig. 23; glossae broadly curved over ventrolaterally, large; paraglossae broadly rounded laterally; anterolateral corners of submentum weakly swollen, median area of basal margin gently rounded, lateral margins of submentum without setae. Legs: hind legs longer than fore- and mid legs, forefemora shorter and slightly fatter to fatter (greater width/length ratio) than mid and hind femora, femora indented on apical 2/5 of inner margin so tibiae can draw partially into femora, maximum width of tibiae 1 1/3 times maximum width of tarsi, inner and outer margins of femora and inner margins of tibiae and tarsi with thick setae, inner basal margin of forefemora with a row of setae, mid and hind tibiae without numerous thick setae on outer margin and medial area, outer margins with scattered long hair-like setae; foreclaws (Fig. 15) weakly hooked and narrow apically, with a basal group of 5–6 narrow pointed denticles along inner margin, denticles slanted, directed anterolaterally, increasing in size apically; and a subapical row of 5 narrow pointed denticles also increasing in size apically. Gills (Fig. 16–18): gills on segments 1–7; ventral lamina of gills 4/5 to subequal to length of dorsal lamina, tracheae of gills branched; gills on segments 2–6 similar (Fig. 17), dorsal lamina with outer basal margin developed anteriorly, ventral lamina with inner basal margin developed anteriorly, apical margin of both laminae with large inner lobe, small outer lobe and a narrow median projection; dorsal and ventral laminae of gill 1 (Fig. 16) lanceolate, slender, gradually tapered apically; dorsal and ventral laminae of gill 7 (Fig. 18) similar, lanceolate, except dorsal lamina wider and longer, ventral portion roughly 4/5 length of dorsal portion, dorsal portion with outer median margin developed and abruptly tapering to apex. From lateral view, posterolateral margins of terga and sterna 8–9 form spines. Caudal filaments: basal 3/10 with clusters of long dense setae forming rows, terminal filament with a row of seta on each lateral margin, cerci with a row of seta on inner lateral margin.

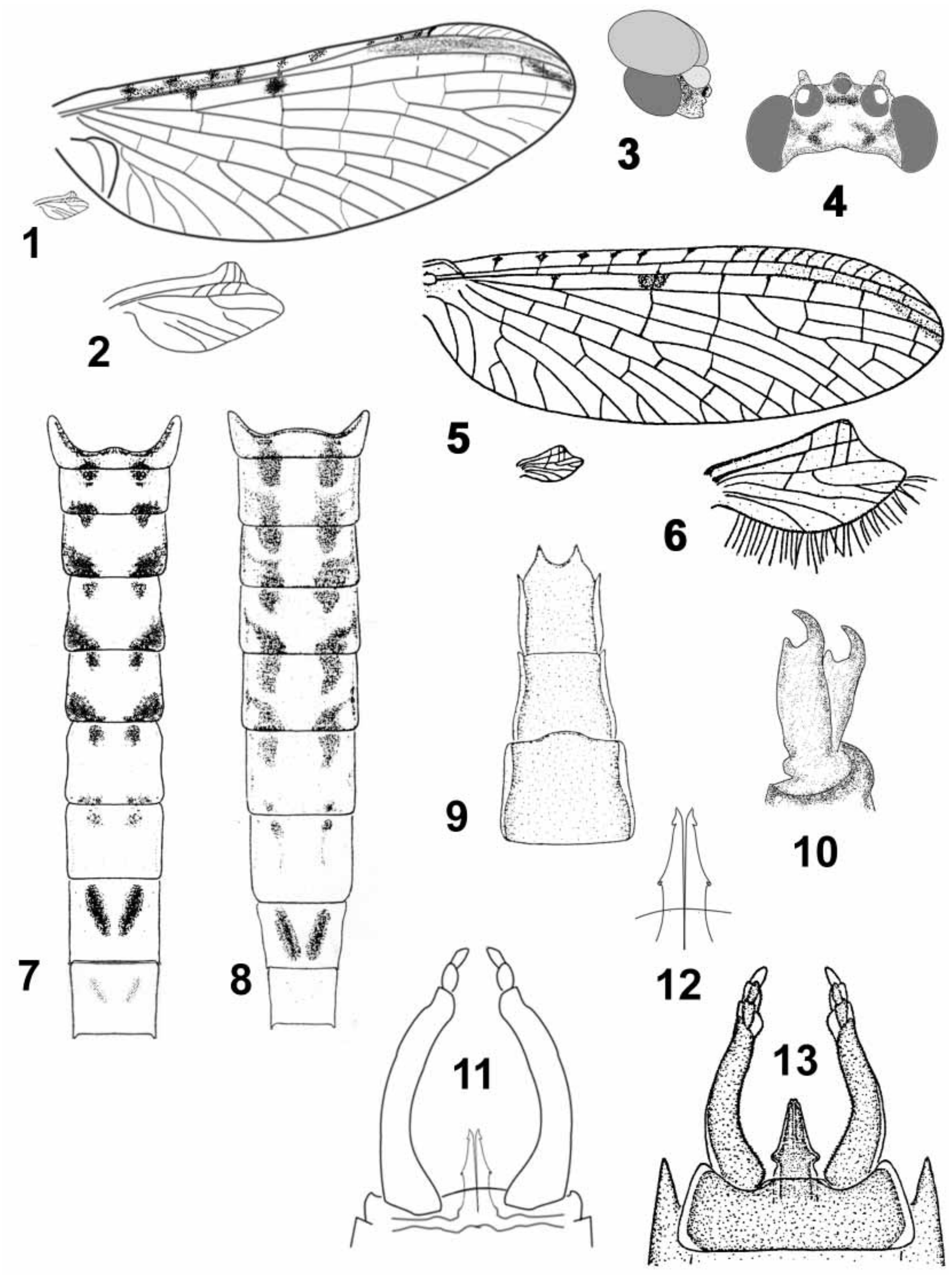
Etymology: Tikuna, a Native American tribal name, feminine.

Discussion: Within the *Terpides* lineage, *Tikuna* is most closely related to *Fittkaulus*, from which it can be distinguished by the following combination of characters. In the imagoes: 1) upper portions of male eyes are on very short, wide stalks; 2) penes are short, basal 1/2 fused, apical 1/2 unfused; mid-lateral margins with projections (Fig. 12). In the nymphs: 1) the two series of denticles in the claws are similar in form and contiguous (Fig. 15); 2) ventral portions of gills 2–6 with large inner and outer lobes on apical margins (Fig. 17); 3) ventral lobes of glossae long and outwardly curved (Fig. 23).

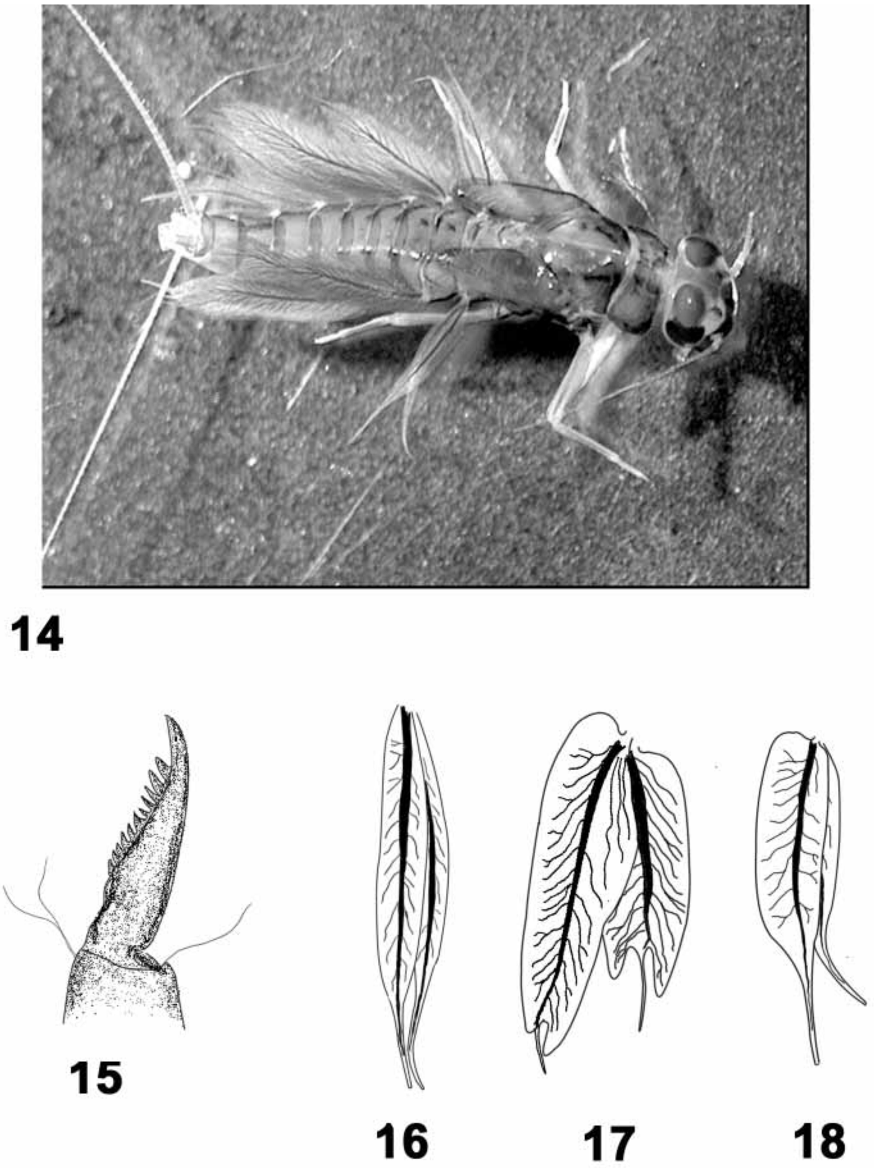
Tikuna atramentum **(Traver) new combination**

(Figs. 1–22)

Choroterpes atramentum Traver 1947:156



FIGURES 1–13. *Tikuna atramentum*, imago and subimago. 1, fore– and hind wings; 2, hind wing, enlarged; 3, head of ♂ imago, lateral view; 4, head of ♀ imago, dorsal view; 5, fore- and hind wings of holotype subimago; 6, hind wing of holotype subimago, enlarged; 7, abdominal terga 1–9 of ♂ imago. 8, abdominal terga 1–9 of ♀ imago. 9, sterna 7–9 of ♀ imago; 10, claws of ♀ imago; 11, genital segments of ♂ imago; 12, penes, enlarged; 13, genital segments of holotype ♂ subimago.



FIGURES 14–18. *Tikuna atramentum*, nymph. 14, nymph (median caudal filament broken); 15, foreclaw. 16–18, abdominal gills on: 16, segment 1; 17, segment 5; 18, segment 7.

Male Imago (in alcohol). Length: body 7.8 mm; forewings, 6.7 mm. Head whitish yellow, antennae translucent. Thorax: nota whitish yellow, submedian longitudinal brownish black stripes extend from anterior margin of pronotum to posterior mesonotum, submedian stripes broken on metanotum; sterna and pleura whitish yellow. Forewings (Fig. 1): stigmatic crossveins not anastomosed to very weakly anastomosed; costal brace yellow; longitudinal veins brownish yellow to hyaline, veins C, Sc and R_1 darker, posterior veins lighter, distal 1/3 of Sc washed with brownish black, basal portion of these crossveins brownish yellow, crossveins of R_1 cell washed with brownish black, wash darker and wider anteriorly, 2 crossveins at base of radial field and 1 median crossvein between R_{4+5} and MA brownish black, remaining crossveins light yellow to hyaline; membrane of C cell with brownish black clouds surrounding anterior portion of crossveins as in Fig. 1, posterior portion of costal crossveins basal to stigma with brownish yellow clouds, basal portion of stigma in C cell with a light reddish brown to brownish black wash; basal crossvein in cell R_2 with cloud distinctly wider anteriorly, median crossvein with a prominent, large, brownish black cloud, apical crossveins with narrow clouds that widen anteriorly; apex of wings with a light yellow band covering apical 1/3 of Sc cell and apex of R_1 cell, a brownish black to reddish brown band continues apically from near apex of vein Sc to apex of wing in radial field just posterior to R_2; remainder of membrane hyaline, translucent. Hind wings (Fig. 2): longitudinal veins and crossveins hyaline, veins C and Sc darker, posterior veins lighter; membrane whitish hyaline, translucent. Forelegs light yellow, inner margin of femora with brownish black, distal, longitudinal streak and small dash near base; remainder of legs pale yellow. Abdomen (Fig. 7): terga whitish yellow; tergum 1 with posterior submedian brownish black marks and narrow brownish black lines along anterior margin; terga 2–5 with anterior and posterior, submedian, and spiracular brownish black marks, brownish black wash continues anterolaterally from anterior margin of posterior marks; tergum 6 with anterior and posterior submedian marks, posterior marks absent on tergum 7; tergum 8 with prominent submedian brownish black marks that converge distally; tergum 9 with light, narrow brownish black submedian washes that converge distally; tracheae semihyaline; sterna whitish yellow. Genitalia (Figs. 11, 12): styliger plate, forceps and penes light yellow. Caudal filaments whitish.

Female Imago (in alcohol). Length: body, 6.4–7.3 mm.; forewings, 6.6–6.9 mm. Head whitish yellow with heavy brownish black wash near compound eyes. Antennae whitish yellow. Thorax: color and marks as in M but with middle of mesonotum washed with tan. Wings: similar to male except C cell of forewings with three large brownish black clouds located basal to large median cloud in R1 cell; hind wings as in Fig. 2. Legs: [broken off and missing]. Abdomen (Fig. 8): terga washed with brownish yellow, darker medially; terga 1–5 with brownish black marks similar to male except marks larger; tergum 6 with large anterior and small posterior submedian marks; tergum 7 with anterior submedian marks and heavy brownish black wash continuing posteriorly from marks; color and marks on terga 8–9 as in male; tergum 8 with posterolateral spines; color of spiracles, tracheae and sterna as in male; caudal filaments whitish.

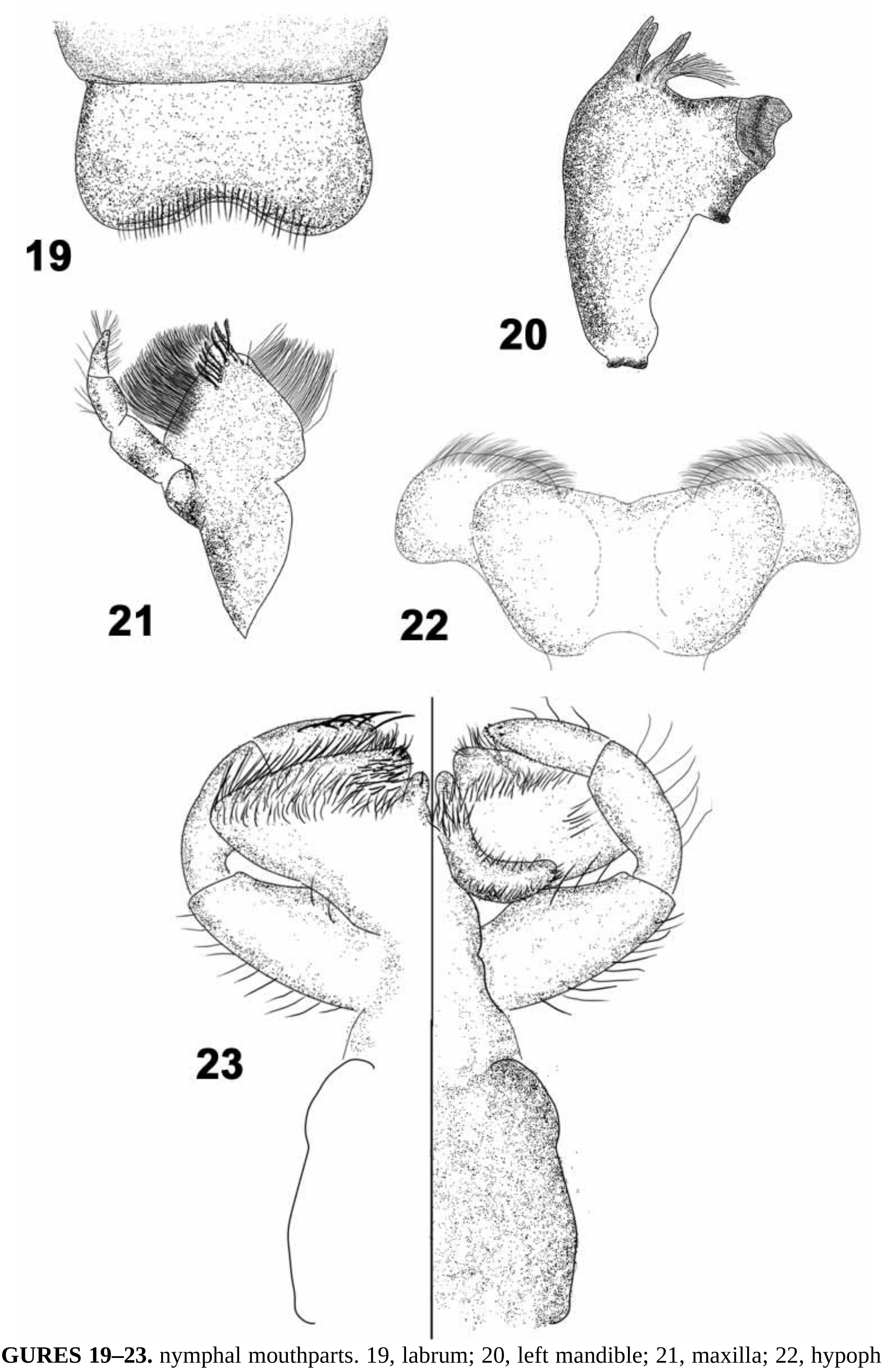
Nymph (in alcohol, Fig. 14). Body length 6.1–7.5 mm. Head brownish yellow to yellowish brown, lateral edges of genae darker. Antennae pale yellow. Mouthparts (Figs. 19–23): labrum with maximum length slightly greater than 1/5 width; anteromedian emargination well developed with 6 very small, apically flattened denticles; segment 2 of labial palpi subequal to length of segment 1; segment 3 of palpi 7/10 length of segment 2. Thorax: yellowish brown, pleura whitish yellow with sclerites yellowish brown; sterna whitish yellow, meso- and metanotum washed with pale brown laterally; brownish black marks as in male imago. Legs brownish yellow, forelegs slightly darker. Abdomen: terga and sterna light yellowish brown, with rear margins darker brown, terga 8–10 darker brown; terga 1–6 and 8 with brownish black maculae as in male imago, terga 1–6 with small posterolateral brownish black diagonal streaks; tergum 10 with brownish-black wash laterally and a pale median area. Gill membrane translucent, tracheae washed lightly to heavily with brownish black. Caudal filaments whitish yellow.

Specimens examined: ♂ subimaginal holotype, COSTA RICA, Río Pedregoso, Feb. 1939, D.L. Rounds; 1 ♀ subimaginal allotype and 1 male paratype (genitalia missing), same data as holotype. Other specimens examined: COSTA RICA: Guanacaste Prov. 1 ♂ imago (INBio) Canton de Nandayure, San Pedro, at light, 8-XI-2002, W. Porras, R.W. Flowers, Y. Cardenas. 1 ♂ imago (INBio) Reserva Monte Alto, Río Nosara, at light, 21-VI-2002, W. Porras, R.W. Flowers. 1 immature nymph, same locality, 22-VI-2002, R.W. Flowers, W. Porras. 1 ♂ subimago, same locality and collectors, 18-VI-2002. 11 ♂, 5 ♀ subimagos (5 ♂, 2 ♀: INBio; 6 ♂, 3 ♀: UCR), Finca Agua Fria, San Pablo de Nandayure, luces, 10-IV-2002, W. Porras. Area de Conservación Guanacaste: Sector Santa Elena: 1 ♀ imago, área serpentina, Malaise trap, 3-IX-2002, R.W. Flowers. 1 ♀ imago, same locality and method, 17-IX-2002. 1 immature nymph, Río Cuajiniquil, 7-XII-2002, R.W. Flowers, M.M. Chavarría. Sector Santa Rosa: 3 immature nymphs, Río Cuajiniquil, 21-XII-2002, M.M. Chavarría. 3 immature nymphs, Río Cuajiniquil, Sendero Cafetal, 15-XII-2002. San José Prov. 6 immature nymphs (UCR), El Rodeo, 850m. quebrada en las instalaciones de UPAZ, 4-10-98.

Distribution (Fig. 24) : Western Costa Rica, primarily on the peninsulas of Santa Elena and Nicoya.

Ecology: All specimens collected during 2002 came from seasonal streams in areas of Costa Rica that experience a four to six-month dry season. The first collection in April near Carmona was at light next to the Río Nandayure which has flowing water nine months of the year; from March to June flow becomes intermittent with some permanent pools and subterranean flow. The mayflies were collected next to the only permanent pool on that stretch of river. Adults and nymphs were found in the Río Nosara in and below the Reserva Monte Alto in June. This stream is small, with moderate to dense shade. Inside the reserve, *T. atramentum* was found in an area of riffles and small pools below a waterfall; the site below the reserve consisted of riffles and a large pool that contained a diverse population of large river shrimp. This area dries completely from the end of February to June.

The San Pedro site in Nicoya, where a single adult male was taken at UV light, is a sparsely populated mountainous area consisting of a mosaic of small farms and ranches and patches of second-growth forest. The light was set up next to a small stream that disappears in the dry season but has abundant water and is prone to spates the during the rainy season.



FIGURES 19–23. nymphal mouthparts. 19, labrum; 20, left mandible; 21, maxilla; 22, hypopharynx; 23, labium: left, dorsum; right, venter.

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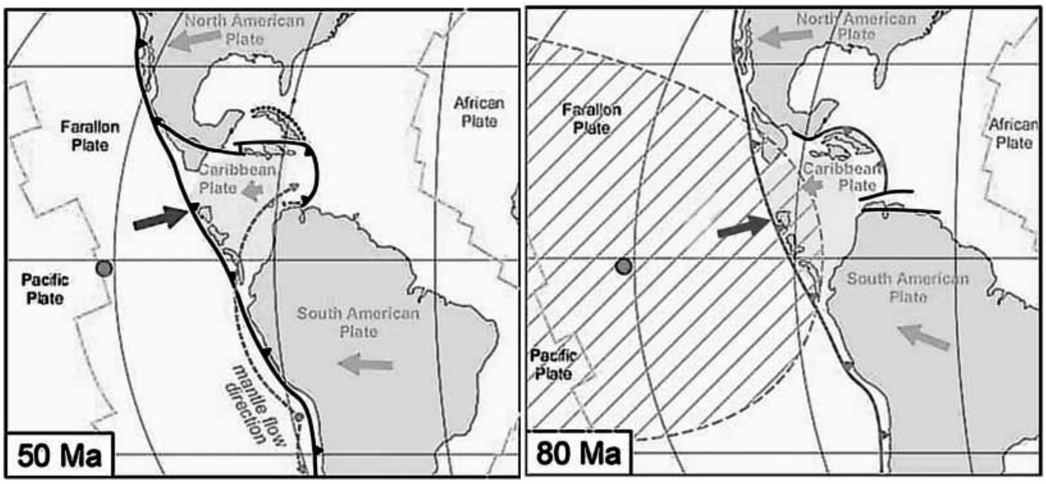

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FIGURES 24–25. 24, Geological map of Costa Rica (redrawn from Abratis 1998) showing terranes of the Nicoya Complex (light grey), localities of recent collections of *Tikuna atramentum* (black squares), and two possible locations for the type locality (question marks). **25**, Reconstruction of development of Lower Central America during the late Cretaceous (80 Ma) and early Tertiary (50 Ma) (redrawn from Meschede 1998). The black arrows point to the northern apex of the Costa Rica–Panamá island arc.

In the Santa Elena Peninsula, the area where adults of *T. atramentum,* where taken in a Malaise trap is on a ridge of serpentine rock in a mixture of grassland and fragments of dwarf forest. This serpentine area is the geologically oldest part of Costa Rica, and soil is unusually nutrient-poor. During the rainy season small streams drain the ridge into the Río Potrero Grande and the Río Cuajiniquil. In early December (a month after the start of the dry season) the Río Potrero Grande was still flowing, but few mayfly nymphs were found. These belonged to the typical flowing-water community (*Thraulodes*, *Baetodes*, *Leptohyphes*) found throughout Costa Rica and Panamá in clean to moderately clean water. By contrast, water flow in the Río Cuajiniquil had almost stopped, but water was still plentiful in numerous pools between rocks. In the place where we found nymphs of *T. atramentum*, nymphs of *Caenis* sp., *Choroterpes* s.s. sp., and *Callibaetis* sp. were abundant. A short distance downstream in a large, waist-deep pool, nymphs of *Ulmeritoides* were collected. The entire mayfly community in the Río Cuajiniquil consisted of species rare or at least uncommon in other areas of Costa Rica.

El Rodeo is a forest fragment in the middle of large cleared agricultural area. The streams here are temporary.

No information other than the name of the river is known for the type locality. There are two "Río Pedregosos" and three "Quebrada Pedregosas" listed for Costa Rica. The best known of these is the Río Pedregoso which flows south from Cerro de la Muerte into the Río Terraba basin near the city of San Isidro de General. The other Río Pedregoso is nearby but flows northwest into the Río Pirrís, which empties into the Pacific Ocean between Punta Judas and Parque Nacional Manuel Antonio. Two of the "quebradas" are located not far away, but in areas that had not yet been colonized and were probably not accessible to travelers in 1939. Interestingly, the third Quebrada Pedregosa is in Nicoya near the town of Jicaral, which was an accessible area in the early 1900's.

Tikuna atramentum apparently has a long emergence period, or is multigenerational with adult emergence taking place throughout the period when water is found in the streams where they live. In Nicoya adults have been found in April, June, and November. In Santa Elena, nymphs found in late December had large wing pads with the wings inside just beginning to darken.

Biogeography

Theories about the origin of the biota of Costa Rica have generally assumed dispersal across a Central American land bridge that was formed by volcanic and tectonic activity sometime during the Pliocene. The Pleistocene was the time of active, two-way dispersal with placental mammals moving into South America while rainforest plants, birds, and insects moved north. This period has sometimes been called the "great American interchange" (McCafferty 1998). South American Ephemeroptera have dispersed asymmetrically northward with 21 genera reaching North America—one into Canada—while only four North American genera have reached South America (McCafferty 1998). For most of these genera, the prevailing hypothesis of movement across a relatively recent land bridge is an adequate explanation for their present phylogenetic and distributional data. However, the distribution and relationships of *Tikuna* suggest an alternate biogeographic scenario in which *Tikuna* could have arrived in the Nicoya Complex and perhaps elsewhere in the early Tertiary, or possibly even the late Cretaceous.

The family Leptophlebiidae is presently divided into three subfamilies the Leptophlebiinae and the Habrophlebiinae of Laurasian origin, and the Atalophlebiinae, of Gondwanian origin. The separation of the subfamilies probably coincided with the separation of Pangaea. Phylogenetic and distributional evidence strongly indicates that the *Terpides* lineage, which consists of the genera *Terpides*, *Fittkaulus*, and *Tikuna* arose on the ancient Guyana and Brazilian Shields and separated from the rest of the Atalophlebiinae at a very early date, possibly in the late Cretaceous or early Tertiary (Savage 1987, Flowers and Domínguez 1991).

All of known localities of *Tikuna*, with the possible exception of the type locality, are on or near the Nicoya Complex, areas of Cretaceous ophiolitic rocks. These were originally of sea floor origin but uplifted to form the Costa Rica–Panamá Arc which became an island chain during the late Cretaceous (Meschede and Frisch, 1998). Localities of ophiolitic areas in Costa Rica and the distribution of *T. atramentum* are given in Fig. 24. While not flowing through part of the Nicoya Complex, the stream at El Rodeo could have been reached by upstream colonization from the ophiolitic area around the Turrubares Mountains. Thus, in the Cretaceous–early Tertiary period, both the *Terpides* lineage and the geologic areas of Costa Rica in and near which *T. atramentum* is still found were both in existence. What is still needed is a geologic mechanism for bringing them together.

In generally accepted scenarios for the formation of Lower Central America, the Nicoya Complex has its northern end close to large nuclear Central American land masses and its southern end quite distant from South America (Donnelly 1985, Smith 1985), a combination which would make any early dispersal northward by South American lineages all but impossible. However, a recent model by Meschede and Frisch (1998) of the formation of the Caribbean Basin postulates a Costa Rica–Panamá island arc that lay across the southern half of the gap between North and South America with its southern terminus very close to continental South America (Fig. 25). In the late Cretaceous–early Tertiary this arc could have enabled *Tikuna* to move from South America to Nicoya and Santa Elena much earlier than the generally accepted scenarios of Central American biogeography postulate. Nor was *Tikuna* necessarily alone; McCafferty (1998) hypothesized, based on phylogenetic evidence, that two other mayfly genera, *Hexagenia* and *Homoeoneuria*, could have had similarly early dispersal histories. The rediscovery of *Tikuna atramentum* raises the intriguing possibility that Costa Rica acquired some of its biodiversity eons before the Great American Interchange.

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