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DIVERSIDAD DE LIBÉLULAS (INSECTA: ODONATA) EN AMBIENTES LÉNTICOS CON DIFERENTE GRADO DE ALTERACIÓN ANTROPOGÉNICA

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado y título de Maestría Académica en Biología

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DEDICATORIA

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RESUMEN

Costa Rica es el país centroamericano donde mejor se conoce la fauna de libélulas (Insecta: Odonata). Sin embargo, los estudios han estado enfocados principalmente en ambientes lóticos, generando un vacío de información en los ambientes lénticos. El incremento de la urbanización impacta en los ecosistemas dulceacuícolas generando cambios en el paisaje y es uno de los impactos antropogénicos más significativos que amenaza a la biodiversidad. Esta investigación se realizó durante un año en seis lagunas: dos urbanas (La Sabana y La Paz), dos semi-urbanas (Lankester y Doña Ana), y dos rurales (CATIE y El Rodeo). El objetivo fue evaluar los ensamblajes de libélulas y relacionarlos con los parámetros ambientales de cada sitio, así como criar larvas con el fin de asociar los estadíos larva-adulto para las especies encontradas. La captura de adultos se realizó por medio de red entomológica, con esfuerzo total de muestreo de 5 horas (9:00-14:00pm). Para el análisis de los datos se realizó un Análisis de Componentes Principales (PCA, por sus siglas en inglés) para identificar los patrones en los lagos usando las variables ambientales y se realizó una prueba de similitud (ANOSIM) para determinar la significancia de los grupos formados. Finalmente se realizó un Análisis de Correspondencias Canónicas (CCA, por sus siglas en inglés) para determinar la relación entre los taxones colectados en cada uno de las lagunas y los datos de las variables ambientales. En total, se recolectaron 644 especímenes adultos de 6 familias, 29 géneros y 51 especies. Las familias con mayor riqueza fueron Libellulidae con 53% (29 spp.), seguido de Coenagrionidae con 25% (15 spp.). Las familias de menor riqueza fueron Lestidae y Gomphidae con una especie cada una. Los géneros más diversos fueron *Micrathyria* (Libellulidae) con 10% (5spp.), seguido de *Argia, Erythemis, Erythrodiplax* con 8% del total de la riqueza de especies (4 spp. cada una). El ANOSIM confirmó que el ensamblaje de grupos es estadísticamente diferente (R=0.68, *p*=0.001). El CCA mostró el efecto de cuatro variables fisicoquímicas en el ensamblaje de los Odonata (χ^2 =0.54, F=2.58, *p*=0.001). Las primeras dos dimensiones del CCA tienen un efecto significativo: CCA1 (χ^2 = 0.23, F=4.44, *p*=0.001), CCA2 (χ^2 = 0.15, F=2.82, *p*= 0.008) y observamos la formación de cuatro grupos. De las larvas criadas en el laboratorio, se lograron asociar especies de las familias Aeshnidae, Libellulidae y Coenagrionidae. De las cuales tres especies: *Acanthagrion speculum, Acanthagrion trilobatum, Anisagrion allopterum* fueron asociadas y descritas por primera vez y se realizó la redescripción de *Neoerythromma cultellatum,* estas especies pertenecen a la familia Coenagrionidae. Nuestros resultados muestran una alta importancia de los ambientes acuáticos urbanos para la conservación de las especies. Un buen diseño en la disposición de lagos con buena calidad del agua, pueden servir como corredor de conexión de las especies entre el paisaje urbano y rural, y de esta manera ayudar a no restringir su distribución. Además, este estudio demostró que la protección y manejo de las lagunas urbanas es esencial para mantener la diversidad de los organismos.

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PREFACIO

Entre los ecosistemas de aguas continentales, los sistemas lénticos, incluyendo los temporales, ocupan una parte relativamente pequeña en el mundo, si se compara con las áreas que cubren los sistemas lóticos (Barrett & Odum 2006, Lukács et al. 2012,). Sin embargo, estos ecosistemas son de gran importancia ecológica (Barrett & Odum 2006, Alonso Eguía-Lis et al. 2014, Ramírez 2010, Gál et al. 2019). Estos sistemas son también conocidos como aguas estancadas, es decir que no presentan corriente continua, sino que están retenidas en un sitio determinado (Rodríguez-Garzón 2012), aunque esto no significa que no tengan entradas y salidas de agua, lo cual va a depender de su tipo de origen (SINAC 2007). Las condiciones ambientales de estos sistemas impactan las especies que habita en ellos y sus interacciones (Barrett & Odum 2006), por lo que la evaluación de su estado es de vital importancia para la conservación de muchas especies.

Los ambientes dulceacuícolas en Costa Rica

Costa Rica posee una gran diversidad de ecosistemas de aguas continentales, en los que, por las características físicas del país, predominan los sistemas lóticos, especialmente ríos y quebradas (Pringle et al. 2016). De los sistemas lénticos se han registrado 510 con una dimensión mayor a 0.1 ha, tanto naturales (lagos, lagunas, lagunas costeras) como artificiales (reservorios y embalses) (SINAC 2007). Estos ambientes se han categorizado de la siguiente manera: 1) de acuerdo al tamaño (superficie y profundidad): lago, laguna, laguneta, laguna costera; 2) considerando la elevación en la que se localizan: llanura (<300 msnm), bajo (300-1000 msnm), alto (1000-2700 msnm) y muy alto (>2700 msnm); 3) según el origen geológico: volcánico, tectónico, glacial; 4) de acuerdo a su funcionamiento a nivel de la cuenca hidrográfica: endorreico o exorreico (SINAC 2007).

Los sistemas ecológicos dulceacuícolas en Costa Rica se encuentran bajo la categoría de humedales que incluye todos los hábitats de agua dulce o salobre (Córdoba et al. 1998) mismos que: “podrán delimitar zonas de protección de determinadas áreas marinas, costeras y humedales, las cuales se sujetarán a planes de ordenamiento y manejo, a fin de prevenir y combatir la contaminación o la degradación de estos ecosistemas.” (Ley Orgánica del Ambiente N.º 7554, 1995, artículo 42, SCIJ 2020). Sin embargo, cabe mencionar que la protección de los sistemas epicontinentales, es decir, aquellas aguas superficiales que se distribuyen en los continentes (*e. g.* lagos, lagunas, ríos, arroyos, entre otros) no considera la vida acuática (SINAC 2007). Es evidente que hacen falta estudios que fundamenten o analicen la importancia de estos sistemas para los diferentes grupos de organismos que habitan los sistemas lénticos de Costa Rica. Estos proporcionarán información para establecer acciones que protejan las comunidades ecológicas y permitirá constituir herramientas para mantener la integridad ecológica.

De los sistemas acuáticos del país, han sido los sistemas lóticos los que han tenido una gran atención por investigadores para realizar estudios en temas ecológicos relacionados con los macroinvertebrados (Springer et al. 2014), entre otros. Mientras que los sistemas lénticos han recibido atención en algunos temas ecológicos y limnológicos (Arroyo 1993, Asch 1996, Bravo & Sánchez 1994, Chaves-Ulloa et al. 2014, Hernández 1990, Umaña-Villalobos et al. 1999, Umaña-Villalobos 2010, Umaña-Villalobos 2014), especialmente en temas de fitoplancton y zooplancton (*e.g.* Umaña-Villalobos 1993, Umaña-Villalobos & Avilés-Vargas 2019).

Por otro lado, debido a las actividades del uso de la tierra, una proporción importante de los sistemas lénticos en Costa Rica han sido drenados o rellenados (SINAC 2007). Otra amenaza para estos ambientes proviene del cambio en el uso de suelo, esto modifica las comunidades de vida acuática y terrestre a su alrededor. Estas alteraciones generan un impacto en las variables ambientales y fisicoquímicas del agua, las cuales son parte influyente sobre la calidad del agua, por tanto, cualquier alteración afecta directamente en las comunidades acuáticas (Hawkins et al. 1982, Roldán 2003, Ocon & Rodríguez 2001, Román-Heracleo 2013). Entre los principales factores que determinan la supervivencia de las poblaciones de macroinvertebrados acuáticos se encuentran factores ambientales como: sustrato, profundidad, sedimentos, materia orgánica proveniente del mismo ambiente, contaminantes tanto industriales como domésticos, además de factores físicos y químicos como temperatura, pH, concentración de sólidos disueltos, oxígeno disuelto, entre otros (*e.g.* Prat & Rieradeval 1998, Paukert & Willis 2003, Reyes 2013).

El orden Odonata es uno de los grupos de macroinvertebrados que, debido a su sensibilidad, en la mayoría de sus especies, sufren alteraciones en sus poblaciones a consecuencia de los cambios en el hábitat acuático y terrestre (*e.g.* Samways et al. 1996, Córdoba-Aguilar & Rocha-Ortega 2019, Juen & Feest 2019, Palacino-Rodríguez et al. 2020). Estos cambios se pueden ver reflejados a corto plazo, mismos que modifican la abundancia, riqueza y composición de sus ensambles, así como la distribución de los organismos dentro del cuerpo de agua.

El orden Odonata: generalidades

El orden Odonata se divide en dos subórdenes: Anisoptera y Zygoptera, morfológicamente fácil de diferenciar (Corbet 1999). Los zygópteros adultos se pueden reconocer por su largo y delgado abdomen y la mayoría de las especies pliegan las alas cuando están perchados. Las larvas se caracterizan por tener el cuerpo esbelto y branquias al final del abdomen, que les ayudan en la respiración y además les sirven para la locomoción (Corbet 1999). Los anisópteros adultos tienen cuerpo robusto, su vuelo es rápido y al posarse siempre mantienen las alas abiertas (separadas). Las larvas suelen ser mucho más robustas en comparación con las de los zygópteros y carecen de branquias caudales externas (Kalkman et al. 2008, Escoto-Moreno et al. 2014).

Las larvas de los odonatos habitan una gran diversidad de hábitats acuáticos, especialmente de agua dulce, solo unas pocas especies toleran condiciones salobres, dos de las cuales viven en marismas y manglares (Kalkman et al. 2008). Se les puede encontrar en aguas con corriente (ríos y quebradas), o aguas estancadas (lagos o lagunas), e incluso en agua contenida en los huecos de los árboles y otros fitotelmata, como las bromelias (Haber et al. 2015). Los adultos son insectos voladores, se encuentran cerca de los ambientes acuáticos y son el estadio encargado de la dispersión y reproducción.

El estadio larval dura desde unas pocas semanas hasta varios años en desarrollarse (Kalkman et al. 2008), dependiendo de la especie y diversos factores ambientales (Corbet

1999). La emergencia se produce fuera del agua, en diversos sustratos: plantas, rocas o en las orillas. La larva sale del agua para que el adulto empiece a emerger, proceso que dura unos minutos desde que rompe la piel hasta que despliega las alas y el abdomen por completo, permitiendo el primer vuelo (Corbet 1999, Kalkman et al. 2008). Los adultos de algunas especies emergen al amanecer o durante el día en momentos con poca incidencia solar (*e.g.* familia Coenagrionidae). En el caso de Anisoptera, por ejemplo, la familia Libellulidae, los adultos emergen durante la noche. Los machos, una vez maduros, establecen territorios a lo largo del ambiente acuático y las hembras a menudo solo regresan al agua para aparearse y ovipositar (Corbet 1999, Kalkman et al. 2008).

Ambos estadios, larval y adulto, son depredadores primarios y secundarios con una amplia gama de estrategias para la captura de sus presas. Regularmente las larvas se mueven poco, esperando que las presas naden cerca para capturarlas. Se alimentan principalmente de invertebrados pequeños, alevines (juveniles de peces) y otros organismos acuáticos (Roldán 1988, Corbet 1999). Tanto las larvas como los adultos juegan un papel importante en el control biológico de otros organismos, ya que son depredadores de otros insectos que pueden ser plagas en cultivos o vectores de enfermedades (Corbet 1999).

Estado del conocimiento del orden Odonata: Taxonomía

Se han identificado 34 regiones a nivel mundial que mantienen una alta diversidad de especies de Odonata y la mayor diversidad se encuentra en los trópicos (Corbet 1999, Kalkman et al. 2008, González-Soriano et al. 2011). En Centroamérica, la Odonatofauna se encuentra representada por 282 especies hasta el momento (Paulson 2020, Román-Heracleo & Springer 2020).

De los países centroamericanos, Costa Rica es el país donde se conoce mejor la riqueza de odonatos (Ramírez 2010). Se han registrado hasta el momento 280 especies (Haber et al. 2015, Haber 2017). De estos registros, en la última década se han descrito varias nuevas especies, principalmente en Coenagrionidae (Garrison & Von Ellenrieder 2017), Libellulidae (Haber 2015) y Gomphidae (Haber 2017, 2019). Además, durante los últimos años se han asociado y descrito las larvas de varias especies, principalmente de las familias Coenagrionidae, Perilestidae y Gomphidae (Román-Heracleo et al. 2018, Román-Heracleo et al. 2019, Román-Heracleo & Novelo-Gutiérrez 2019, +-Heracleo et al. 2020, Novelo-Gutiérrez & Gómez-Anaya 2019). La asociación de los estadios larvales con los adultos permite llenar el vacío de información que existe en la taxonomía del grupo. Realizar las asociaciones y a su vez descripciones de las larvas, permitirá generar información para llenar los vacíos de conservación de las especies, así como facilitar información que permita su aplicación de manera más específica en estrategias de conservación y su uso como bioindicadores de los ambientes acuáticos.

Perturbaciones en los ambientes acuáticos y los odonatos como bioindicadores

La integridad de los ecosistemas de aguas superficiales y su diversidad biológica cada vez está más amenazada por las actividades humanas en todo el mundo (Gómez-Anaya 2008). La pérdida y fragmentación de hábitats están consideradas dentro de las principales causas de la crisis de biodiversidad, generando patrones de distribución discontinuos en las especies (WWA 2020). La respuesta a la variación de las condiciones ambientales que determinan la calidad de sus hábitats es parte de las consecuencias que lleva en muchos casos a la extinción local de especies (Santos & Telleria 2006). Los cambios drásticos en las variables ambientales son considerados disturbios en los ecosistemas de agua dulce y afectan la variación espacial y temporal de los procesos ecológicos (*e.g*. Dorji 2014, Kohlmann et al. 2015, Da Silva et al. 2016, Gutiérrez-Fonseca 2016).

Diversas especies del orden Odonata son particularmente vulnerables a las perturbaciones antropogénicas, especialmente aquellas especies asociadas a la vegetación ribereña (Samways & Staytler 1996, Corbet 1999). Las especies que presentan un amplio rango de sensibilidad a las alteraciones en la estructura y calidad del hábitat, responden con cambios en sus poblaciones de manera muy rápida, mismos que se ven afectados además por la presencia de vegetación acuática (macrófitas) (Samways & Staytler 1996, Paukert & Willis 2003, Harabis & Dolny 2011). Otro factor importante es la composición fisicoquímica del agua, la cual está relacionada directamente con la capacidad de mantener sustancias sólidas y gaseosas en solución que son fundamentales para el desarrollo de la biota (Soler & Mora 1993).

Los cambios que están sufriendo estos ambientes, a consecuencia de los impactos antropogénicos e incluso por el calentamiento global, limita el asentamiento de muchas especies de odonatos (Sánchez et al. 2009). Estas afectaciones restringen la colonización de sus especies, impactando en su conservación (Corbet 1999, Córdoba-Aguilar & Rocha-Ortega 2019). Debido a estas características, varios autores proponen que pueden ser usados como bioindicadores de la integridad de los ecosistemas (Gómez-Anaya et al. 2011, García-García et al. 2016).

En la evaluación de los sistemas acuáticos se han utilizado mediciones de factores fisicoquímicos, así como la abundancia y composición de las comunidades planctónicas, perifíticas y bentónicas (Rodríguez-Garzón 2012). De estas comunidades, los macroinvertebrados se han utilizado para evaluar la calidad del agua, seguidos por las algas, protozoos, bacterias, peces, macrófitas, hongos y virus (Friberg et al. 2011). Los macroinvertebrados presentan un amplio rango de tolerancia a la contaminación orgánica, además de una respuesta rápida a los cambios en la estructura del ensamblaje. Tienen efectos de bioacumulación, exhiben mutaciones que se pueden ver reflejadas en la deformación o cambios en las estructuras físicas de los organismos y si el sistema está muy dañado, estos organismos llegan a desaparecer o se desplazan a otros cuerpos de agua (Lavilla et al. 2010). Los macroinvertebrados se muestrean fácilmente, tienen una distribución cosmopolita y su identificación es relativamente fácil (Roldán 2003, Segnini 2003), características que los hace idóneos para la realización del biomonitoreo.

De los macroinvertebrados usados como bioindicadores, el orden Odonata, de los órdenes mejor conocidos (Ramírez 2010); es uno de los grupos que son ampliamente utilizados, ya que se les encuentra en una gran diversidad de ambientes acuáticos, además de tener un amplio rango de sensibilidad a los impactos del ambiente (Springer et al. 2014). Los diferentes índices utilizados para la evaluación de los ambientes acuáticos están basados en la taxonomía a nivel de género e incluso algunos índices solo utilizan información a nivel de familia (Barbour et al. 1999). Sin embargo, este nivel de especificidad agrupa los diferentes taxones en un solo valor, incluso cuando existen géneros que tienen especies con diferentes grados de tolerancia a los impactos o cambios de su ambiente. Considerando los diferentes grados de sensibilidad que presentan las especies, es importante llevar estos índices al nivel más alto de especificidad: especie. Para esto, es importante realizar las asociaciones larva-adulto que permite la descripción de las larvas a nivel de especie y a su vez, actualizar los índices al nivel más específico que permitirá la evaluación de los ambientes acuáticos con una mayor precisión. Al mismo tiempo, el estudio de los odonatos en su estadio adulto como indicadores de diversas perturbaciones, p. ej., impactos antropogénicos, permite generar información integral entre los ecosistemas acuático y terrestre que se puede aplicar para implementar estrategias que ayuden en la conservación.

Justificación y objetivos

A pesar de los estudios realizados, en Costa Rica aún existe un vacío de conocimiento sobre los odonatos, especialmente en los ambientes lénticos, muchos de los cuales presentan diferentes grados de impacto antropogénicos generados por cambios en el uso de suelo. Por lo tanto, surge la pregunta de cuáles factores influyen en la diversidad de las especies de odonatos que viven en los ambientes lénticos. Para contestar esta pregunta, nos planteamos evaluar los ensamblajes de odonatos en ambientes lénticos con diferentes grados de perturbación antropogénica en la zona central de Costa Rica. Para esto, se identificaron las características ambientales acuáticas y terrestres que pueden estar influyendo en la presencia de las diferentes especies de odonatos. También se determinó la asociación entre el ensamblaje de odonatos con las características de los distintos ambientes lénticos estudiados, incluyendo el uso de suelo para saber cuáles son las especies que se encuentran asociadas a estas características.

Objetivo general

Evaluar los ensamblajes de libélulas (Insecta: Odonata) en ambientes lénticos con diferentes grados de perturbación antropogénica en la zona central de Costa Rica.

Objetivos específicos

- Determinar las especies asociadas a los ambientes lénticos, según su grado de perturbación antropogénica.
- Identificar las características ambientales acuáticas que influyen en la presencia de las especies de odonatos.
- Identificar las características ambientales terrestres que influyen en la presencia de las especies de odonatos.
- Valorar la utilidad de los odonatos como posibles indicadores de la conservación de los ambientes lénticos en Costa Rica.
- Asociar los estadíos ninfales con sus respectivos adultos para las especies de odonatos encontrados.

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ARTÍCULO 1.

Diversity of dragonflies and damselflies (Odonata) in lentic environments in Costa Rica and their use as indicators of anthropogenic alteration

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INTRODUCTION

Costa Rica hosts a great diversity of freshwater ecosystems. The geographical characteristics of the country allow the predominance of lotic systems, especially rivers and streams (Pringle et al. 2016). Of the lentic systems, 510 have been registered with a water surface greater than 0.1ha, including natural (lakes, lagoons, coastal lagoons) and artificial systems (such as reservoirs) (SINAC 2007). In these environments, a variety of ecological and limnological studies have been carried out (e.g. Arroyo 1993, Asch 1996, Bravo & Sánchez 1994, Hernández 1990, Umaña-Villalobos & Jiménez 1995, Umaña-Villalobos et al. 1999, Umaña-Villalobos 2014b, Umaña-Villalobos & Farah-Pérez 2018). Many of which have been focused mainly on phyto and zooplankton (Gocke et al. 1981, Haberyan et al. 2003, Chaves-Ulloa et al. 2014, Umaña-Villalobos 2014a, Umaña-Villalobos & Avilés-Vargas 2019). However, few studies are related to benthic macroinvertebrates in Costa Rican lakes and lagoons, focusing mainly on ecological issues (Wright & Ruiz 1993, Jiménez & Springer 1993, 1996, Sibaja-Cordero & Umaña-Villalobos 2008, Trama et al. 2009, 2017). Other studies focus on taxonomic descriptions of aquatic insects in lakes and lagoons (e.g. Herrera 2013, Pacheco et al. 2014), with several on the order Odonata (Paulson 2009, Román-Heracleo & Novelo-Gutiérrez 2019, Román-Heracleo et al. 2019, Román-Heracleo et al. 2020).

Odonates, commonly known as dragonflies and damselflies, are an important part of the aquatic communities that can be found inhabiting lentic systems, especially due to their role as predators (May 2019). Some factors that limit the survival of their larval populations are: type of substrate, depth, amount of sediments, amount of organic matter, industrial or domestic pollutants and physicochemical variables such as temperature, pH, concentration of dissolved solids, dissolved oxygen (Prat & Rieradeval 1998, Paukert & Willis 2003, Reyes 2013). As a group, odonates show a wide range of sensitivity to anthropogenic disturbances, with some species showing high tolerance levels, while others are highly sensitive, especially those species associated with riparian vegetation (Samways & Staytler 1996). The changes in their assemblages can be seen reflected in the short term, causing changes in species richness, abundance and composition, including changes in the distribution within the water body (Corbet 2004). These characteristics makes this group especially useful as bioindicators, both for aquatic as well as terrestrial environments, but especially in lentic ecosystems. In addition, they play an important role in the biological control of other organisms, since they are primary and secondary predators of other insects that can be pests in crops or disease vectors (Corbet 1999).

The expansion of urban areas is one of the most significant anthropogenic effects on landscape (Villalobos-Jiménez 2016), and this is also true for many tropical ecosystems, which have been affected by a variety of anthropogenic activities. Therefore, it is necessary to evaluate the communities of existing organisms in these environments, especially aquatic ecosystems, which are among the most threatened tropical ecosystems (Cantonati et al. 2020). Therefore, the question arises about which anthropogenic factors influence the diversity of the dragonfly and damselfly species that live in lentic environments in urban lakes in Costa Rica. To answer this question, the objective of this research was to evaluate the assemblages of Odonata in lentic environments with different degrees of anthropogenic disturbance in the central area of Costa Rica. This led us to 1) determine the species associated with lentic environments, according to their degree of anthropogenic disturbance. 2) identify the aquatic and terrestrial environmental characteristics that influence the presence of odonate species; 3) to assess the usefulness of dragonflies and damselflies as possible conservation indicators of lentic environments of Costa Rica.

MATERIALS AND METHODS

Study sites. Study sites are located with a maximum distance of 67.35 km between the sites within and around the central valley of Costa Rica, between 611 m.a.s.l and 1369 m.a.s.l. The central valley is influenced by the conditions of the Pacific coast slope, with two pronounced seasons, a dry season from December to April and a rainy season from May to November. Mean temperature is 22°C, ranging from 11°C to 27°C, with annual rainfall of 2300mm on average (IMN 2020). The eastern valley, has more rainy days, as a result of greater Caribbean influence, making the dry season less pronounced. The country has a population of 5 022 000, with a population density of 98 inhabitants / km^2 (INEC 2020). Over 50% of the inhabitants live in the Central Valley, where aquatic environments are heavily influenced by urban growth (Villalobos-Jiménez et al. 2016, Kondratyeva et al. 2020).

We selected six lakes, three within the Central Valley (San José Province) and three towards the southeast (Cartago Province) (Fig. 1). The selection was made according to the gradient of urbanization in the surrounding area: two from rural areas (low impact), two from semi-urban and two from urban areas (Table 1).

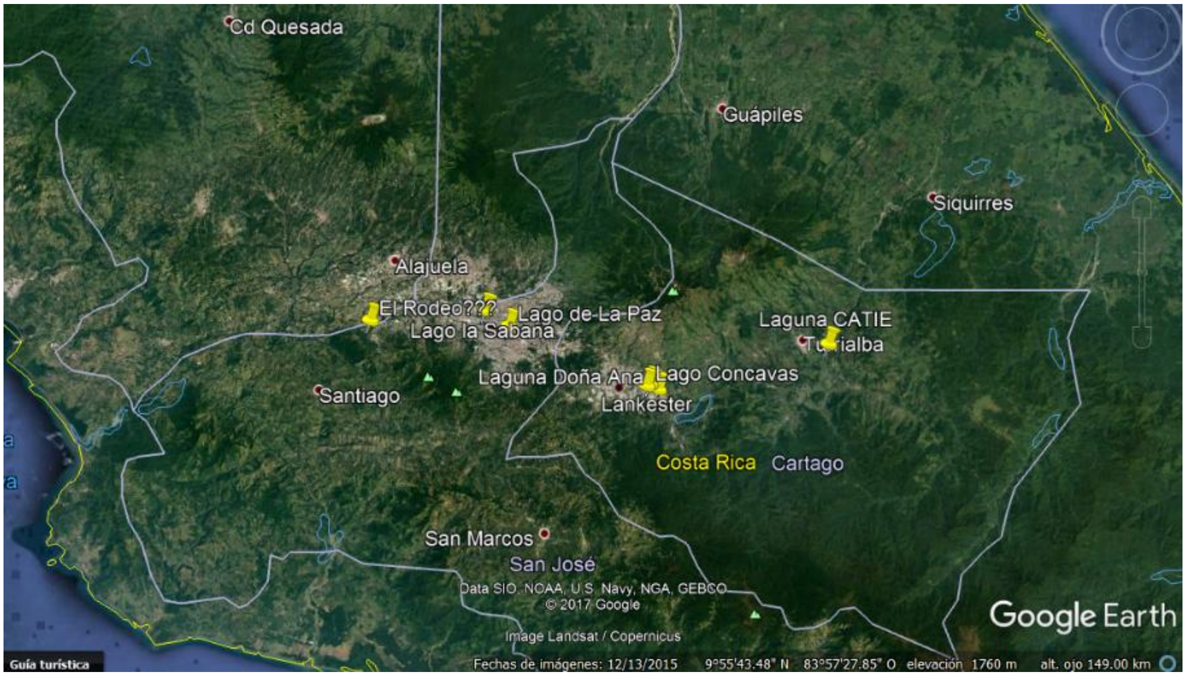

Figure 1. Geographic location of the six sampling sites (lakes) in the central area of Costa Rica.

Table 1. Location and geographical data of sampling sites (lakes) in the central area of Costa Rica.

No.	Name of sampling site (code)	Location				
		Province	Urbanization Level	Altitud (m a.s.l.)	Latitude	Longitude
1	CATIE (CAT)	Cartago	Rural	611	9°53’26.17”N	83°39’16.14”W
2	El Rodeo (ER)	San José	Rural	746	9°55’19.62”N	84°15’18.56”W
3	Doña Ana (DA)	Cartago	Semi-Urban	1345	9°49’58.51”N	83°52’41.19”W
4	Lankester (LAN)	Cartago	Semi-Urban	1369	9°50’24.4”N	83°53’21.55”W
5	La Sabana (LS)	San José	Urban	1132	9°56’09.05”N	84°06’09.64”W
6	La Paz (LP)	San José	Urban	1137	9°54’52.84”N	84°04’22.29”W

Characterization of lakes

The sampling sites (Fig. 2) were characterized by descriptive variables for visual observation *in situ* (Table 2). CATIE, a rural site, presents a mostly natural margin with an inclination of 90°approximately, with arborea and arbustiva terrestrial vegetation; within an agroforestry landscape. It has grassy vegetation along the shoreline and aquatic vegetation is represented by submerged, emergent, free-floating and rooted-floating species, occupying on average 85% of the water surface; the solar incidence on the water is 90%. This lake is colonized by different species of vertebrates: birds, fish, amphibians and reptiles (including caimans). El Rodeo, rural site, surrounded by primary forest; mixed natural and artificial margin, with grass along the shore and without aquatic vegetation with solar incidence of 100% and colonized by vertebrates such as birds, fish and arthropodos such as crustaceans. Doña Ana, semi-urban, recreational park. It presents floating aquatic plants, woody plants, as well as herbaceous. Aquatic plants cover 100% of the water surface and the solar incidence is 100%. The margin is completely artificial (concrete) and colonized by other organisms such as birds, crustaceans, tadpoles. Lankester lake lays within botanical garden within an semi-urban area, the shore line has low grassy vegetation and it is under 100% solar incidence: 75% of the water surface is covered by floating and rooted plants and vertebrates that can be found are waterfowl and fish. La Sabana, urban site it is a park that allows navigation; it has a mixed margin (natural and concrete) with grass on the litoral. The aquatic plants, mainly lilies, cover only 2-3% of the water body and is an environment that is in the process of reforestation of the terrestrial vegetation. The vertebrates that inhabit this lake are birds, turtles and fish. La Paz, urban site, is another recreational park where navigation is allowed. Its margin is artificial (concrete) followed by grass, it does not present aquatic plants, but grass that is flooded when the water level rises. Other organisms such as birds and fish colonize it. All the sites present different assemblages of macroinvertebrates as part of their aquatic fauna, including non native crayfish in Lankester and El Rodeo.

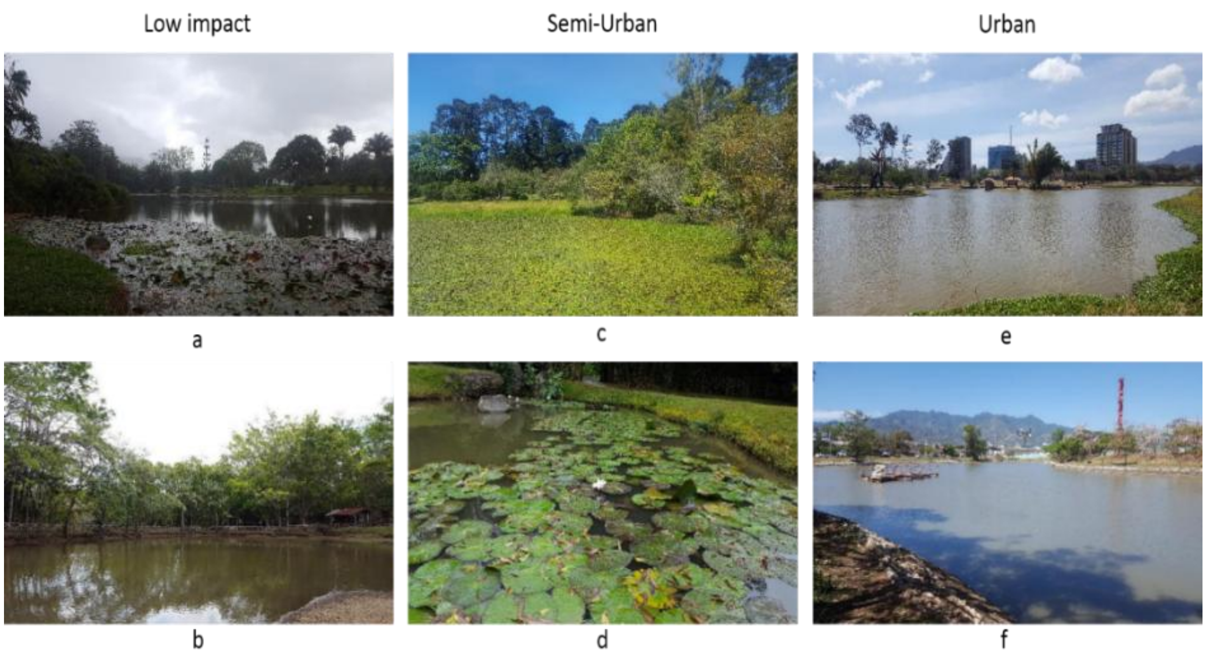

Figure 2. The different lakes sampled in this study. a) CATIE (R), b) El Rodeo (R), c) Doña Ana (SU), d) Lankester (SU), e) La Sabana (U), f) La Paz (U).

Table 2. Data recorded for the different sampling sites, including environmental factors in both aquatic and terrestrial environments.

CHARACTERIZATION OF THE ENVIRONMENT	
Aquatic	**Land**
pH	Relative humidity
Dissolved oxygen	Air temperature
Conductivity	Type of vegetation (grasses, shrubs, trees, etc.)
Temperature	Shading area and area with light incidence (%)
Type of substrate (muddy, rocky, etc.)	Activity around the body of water (land use: agricultural, urban, etc.)
Presence of other aquatic organisms (birds, fish, tadpoles, etc.)	Margin structure (degree of inclination)
Presence and % surface occupied by aquatic plants (high and low emergent, free-floating, rooted floating, submerged, etc.; according to Crow 2002 classification).	Type of margin (natural – *eg.* roots, versus artificial – *eg.* stone)

Field sampling. We sampled each lake along its shoreline, monthly during 2018 and terrestrial and aquatic environmental data were taken to characterize each study site (Table 2). The physical and chemical variables were recorded *in situ* using a multiparameter meter (Model YSI Pro 20) for measure dissolved oxygen and temperature and HANNA HI98130 for measure pH and conductivity. Terrestrial vegetation was characterized according to Müller-Dambois & Ellenberg (1974), within a radius of 500 meters around the waterbody.

Sampling of adults, preservation and identification. At each sampling site, adults were captured by walking parallel to the shoreline of each lake (Butler & deMaynadier 2008), for a total sampling time of 5 hours (9:00-14:00). In order to assure an inventory of the odonates from each lake, during the first sampling campaign we collected representative adult specimens from all odonate species that could be observed. In the following campaigns, we used binoculars to record all known species, and we captured only those new species, which were not collected during previous campaigns. Also, we took pictures from all species, to record their coloration. Collected specimens were placed in wax paper sachets and sampling data were taken for each specimen collected. Envelopes with specimens were placed in a small, hard plastic box to prevent damage to the material and thus facilitate transport to the laboratory for preservation and subsequent identification. In the laboratory, collected specimens were injected or immersed in acetone (trademark J. T. Baker) to maintain the coloration pattern of the specimens and guarantee their preservation. Subsequently, the specimens were placed in envelopes or paper triangles and left for a minimum of 24 hours in acetone (Tennessen 2019). Species identifications was done with specialized taxonomic keys (Esquivel 2006, Garrison et al. 2006, 2010; Garrison & Von Ellenrieder, 2015, 2017). Identifications were corroborated by expert taxonomists: Dennis Paulson, William A. Haber, Enrique González-Soriano, Javier Muzón and Federico Lozano.

Sampling larvae, preservation and taxonomic determination. Larvae were collected to ensure that species found in the surroundings as adults also inhabit the same water body, we using a hand net and the samples are taken in the lakeside. Samples were transported to the laboratory for later identification, and collected larvae were preserved in 70% alcohol, in 1-3 ml vials, sealed with cotton. For final preservation, the vials were placed in hermetic glass jars previously filled with 70% alcohol, following known preservation guidelines for larvae (Ramírez 2010). Identification was done with taxonomic keys to genus level (Novelo-Gutiérrez 1997a, b, Ramírez 2010, Novelo-Gutiérrez et al. 2018) and corroborated by Alonso Ramírez and Rodolfo Novelo-Gutiérrez. All specimens are deposited in the aquatic entomology collection of the Museum of Zoology of the University of Costa Rica (MZUCR).

Statistical analyses. We used principal component analysis (PCA) to identify patterns of urban lakes using the environmental variables. PCA ordinations were conducted on log-transformed data from each sampling date. The PCA is a technique that can help reduce the dimensionality of complex data sets. We used an analysis of similarity (ANOSIM) test to determine the significance of the groups formed in a non-metric multidimensional scaling (nMDS, not show). Followed by a similarity percentage analysis (SIMPER, not show) to determine which species contributed the most to the differences among those groups in nMDS that were supported by the ANOSIM test. This latter test was performed using Bray-Curtis distance and 9999 permutations. Finally, we used the indicator value (IndVal, with

5000 permutations. This test show which species were the principal ones in the composition of each lake, determining the species that were important for the composition of each site (De Cáceres et al. 2012).

We use a Canonical Correspondences Analysis (CCA) to determine the relationship between the taxa collected in each of the lakes through the sampling dates and the environmental variables. CCA has the advantage over methods of indirect gradient analysis of allowing integrated analysis of both taxa and environmental data. A CCA was performed to determine the degree of association between environmental variables and the abundance and distribution of species in the lakes. The CCA allowed us to identify the most important environmental variable related to the species in our study sites. The optimal value of the environmental variables for each species was determined by calculating the weighted average based on their abundance at each site (Leps & Smilauer 2003). To determinate if we most use the CCA (Canonical Correspondences Analysis) model, we analyzed the multicollinearity among environmental variables with Variance Inflation Factors (VIF). If VIF is >10 significant, variables were collinear with one another and values of ANOVA were significative.

The analyses were performed using the R.3.6 software program with different libraries: ANOSIM, SIMPER and Variance Inflation Factors (VIF) was calculated with function of the *vegan* package. ANOVA test was calculated with the *vif* function in the car package. Principal Components Analysis (PCA) was make with *prcomp()* function of the *stats* package and *fviz_pca_biplot()*function of *factoextra* package. Normality test was calculated with *Shapiro-test()* of *stats* package. For Indicator Value we use the function *multipatt()* of *indicspecies* package; non-metric multidimensional scaling (nMDS) *nmds* function of labdsv package. The canonical Correspondence Analysis (CCA) was made using a mix of functions: *geom_label_repel()* function of *ggrepel* package and *decostand()* function of *vegan* package. The graphics were made with *ggplot2* package.

RESULTS

Environmental characteristics

Physicochemical conditions show variations between the sampling sites (Table 3). Water temperature ($F=4.51$, $p=0.001$), dissolved oxygen ($F=6.83$, $p< 0.001$) and conductivity ($F=7.85$, $p= <0.001$) differed between sampling sites. However, no significant differences were observed in pH ($F=0.86$, $p=0.52$). Water temperature ranged from 17 to 28.8ºC; the highest temperature was observed in October in CATIE (Rural-Low impact), and the lowest observed in Doña Ana (Semi-urban) in February. Dissolved oxygen varied from 0.5 to 8.8 mg L^{-1} across the sampled points, and was highest in CATIE, in June during wet season and lowest in Doña Ana in November. Specific conductivity ranged from 33 to 646 µS cm^{-1} and was high in La Paz (urban pool) in dry season, CATIE recorded the lowest in December. The pH value varied from 5.5 to 8.8; the lowest record in CATIE in October and the highest value is recorded in La Paz (urban pool) in August, wet season.

Table 3. Mean (±SD) of environmental variables of the six urban lakes (U), semi-urban (SU) and rural (R) of the central area of Costa Rica

Site	Season	Temperature (ºC)	pH	Dissolved Oxygen (mg L^{-1})	Conductivity (µS cm^{-1})
CAT (R)	Dry	26.02 (2.35)	6.66 (0.42)	3.04 (1.46)	147.62 (144.74)
CAT (R)	Wet	26.64 (1.94)	6.84 (0.84)	5.04 (2.37)	42.60 (5.13)
ER (R)	Dry	24.72 (1.39)	6.78 (0.17)	3.78 (1.30)	267.00 (13.14)
ER (R)	Wet	25.53 (1.69)	6.58 (0.46)	3.73 (1.03)	211.00 (28.39)
DA (SU)	Dry	22.44 (3.59)	7.08 (1.03)	2.74 (2.51)	83.70 (39.47)
DA (SU)	Wet	22.18 (2.43)	6.66 (0.75)	1.74 (0.84)	64.80 (14.48)
LAN (SU)	Dry	22.06 (2.79)	7.02 (0.63)	4.80 (2.74)	224.60 (54.27)
LAN (SU)	Wet	23.54 (1.28)	6.90 (0.81)	5.26 (1.76)	178.80 (50.57)

LP (U)	Dry	22.92 (2.02)	6.75 (0.68)	5.35 (1.26)	269.00 (190.17)
LP (U)	Wet	25.38 (1.24)	6.93 (0.69)	6.15 (0.93)	183.00 (100.10)
LS (U)	Dry	23.72 (2.99)	7.18 (0.41)	6.44 (1.15)	82.20 (19.99)
LS (U)	Wet	25.32 (2.38)	7.20 (0.95)	5.64 (1.53)	84.20 (36.24)

Physicochemical patterns of lakes

Principal component analysis resulted in a 2D (PC) solution, which combined explained 69.0% of the variance. Principal component one (PC1) contributed 40.1% of the variance and was mostly composed of pH and dissolved oxygen. Principal component two contributed 28.9% of the variance and was positive loaded on temperature. PCA effectively separated our study sites (Fig. 3). The PC1 revealed the existence of a first broad group that encompassed urban lake from La Sabana in both seasons, wet and dry, influenced positively by pH and dissolved oxygen and they have negativity association with conductivity. A second group was also present that encompassed for Lankester, CATIE and La Paz, lakes of three level of urbanization, this group was positivity influenced by temperature. PC2 revealed a third group, which was affected positively by the levels of conductivity and negatively by dissolved oxygen and pH, this group was formed by one urban lake: La Paz in dry season, and two rural lake: El Rodeo in both season and CATIE in dry season.

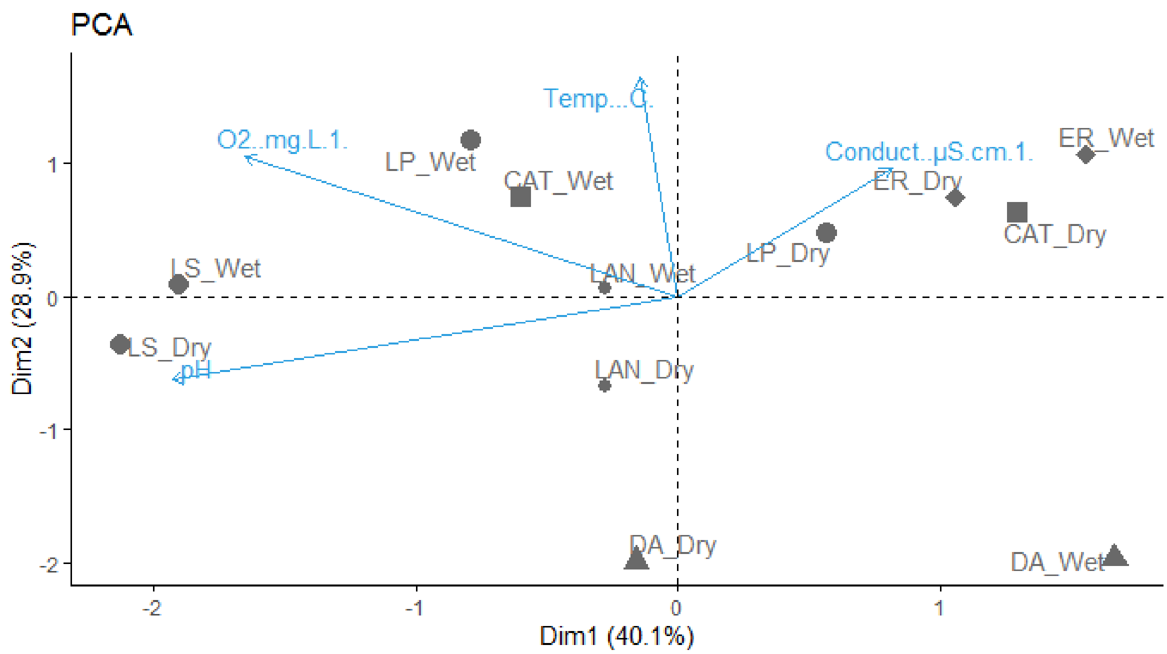

Figure 3. Principal Component Analysis (PCA) ordination plot based on environments variables – temperature, pH, conductivity (Conduct), dissolved oxygen (O_2).

Odonata assemblages

We registered a total of 644 specimens, belonging to six families, 29 genera and 51 species (Table 4a, b). The family with greatest species richness was Libellulidae, with 53% (29 species), followed by Coenagrionidae with 25% (15 species). The family with least richness was Lestidae and Gomphidae with 4% each (1 species each). The most diverse genus was *Micrathyria* (Libellulidae) with 10% (5 species), followed by *Argia*, *Erythemis*, *Erythrodiplax* with 8% each (4 species each one). The lake with greatest species richness was the rural site CATIE with 48% of the total species richness (24 spp.); others sites showed similar species richness: the rural site El Rodeo showed 28% (14 spp.), while the semi-urban sites: Lankester had 32% (16 spp.) and Doña Ana 28% (14 spp.). Urban sites: La Sabana presented 30% (15 spp.) and La Paz showed the least number of species with 24% of the total species richness (12 spp.).

The taxonomic richness varied during the year for each sampling site without any clear pattern (Fig. 4a) and between sites (Fig. 4b). CATIE had the greatest richness during

December, with 19 species registered; Doña Ana had two peaks, one in June, with 8 species, and the next in September and October with 8 and 7 species, respectively. Lankester had an increasing pattern during the months of May, June and August, going from 9, 13 to 13 species by August. La Sabana park showed a peak during the months of August and September, with 14 species for each month; while for February, March and April the richness was 1, 4, 4, respectively. Finally, the lake located in La Paz park had its greatest richness in September and December with 9 and 10 species observed, respectively.

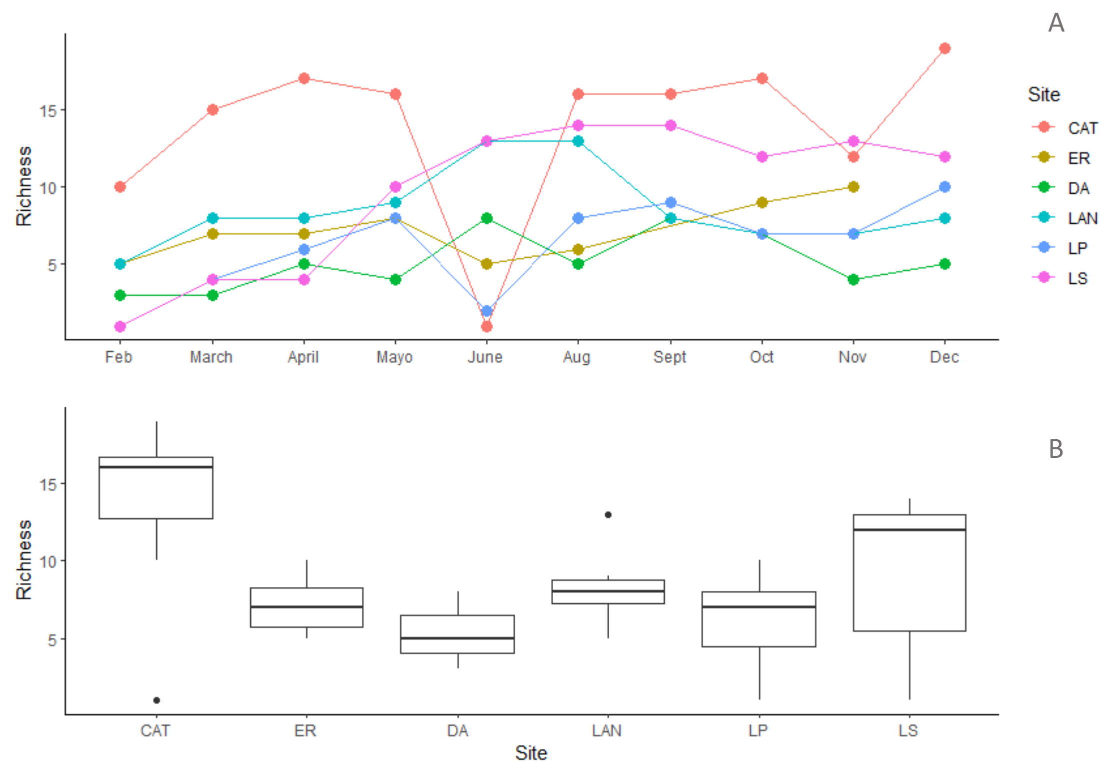

Figure 4. A) Variation of species richness of adult Odonata over time (Feb. – Dec. 2018) and B) between sites (rural: CAT, ER; semi-rural: DA, LAN; urban: LP, LS).

Table 4a. Presence of species of Zygoptera in urban lakes (U), semi-urban (SU) and rural (R) of the central area of Costa Rica, over sampling period (Feb – Dic 2018).

Family	**Genera**	**Species**	**CATIE (R)**	**EL RODEO (R)**	**DOÑA ANA (SU)**	**LANKESTER (SU)**	**LA SABANA (U)**	**LA PAZ (U)**
Calopterygidae	*Hetaerina*	*H. cruentata*				x		
Coenagrionidae	*Acanthagrion*	*A. speculum*	x					
		A. trilobatum		x				
	Anisagrion	*A. allopterum*			x	x		
	Argia	*A. anceps*	x		x	x		x
		A. ellongata			x	x		
		A. pulla		x				
		A. translata		x				
	Enallagma	*E. civile*					x	x
		E. novaehispaniae						x
	Ischnura	*I. capreola*	x		x	x	x	x
		I. ramburii	x	x	x	x	x	x
	Neoerythromma	*N. cultellatum*	x	x				x
	Telebasis	*T. digiticolis*	x					
		T. filiola	x					
		T. salva	x					
Lestidae	*Lestes*	*L. tenuatus*			x	x		

Table 4b. Presence of species of Anisoptera in urban lakes (U), semi-urban (SU) and rural (R) of the central area of Costa Rica, over sampling period (Feb – Dic 2018).

Family	Genera	Species	CATIE (R)	EL RODEO (R)	DOÑA ANA (SU)	LANKESTER (SU)	LA SABANA (U)	LA PAZ (U)
Aeshnidae	*Anax*	*A. junios*			x**			
	Gynacantha	*G. tibialis*	x**					
	Remartinia	*R. luteipennis*			x	x		
	Rhionaeschna	*R. jalapensis*				x		
Gomphidae	*Aphylla*	*Aphylla* sp.		x				
Libellulidae	*Brachymesia*	*B. furcate*	x				x	
	Cannaphila	*C. vibex*				x		
	Dythemis	*D. nigra*					x	
		D. sterilis	x	x		x		x
	Erythemis	*E. attala*	x					
		E. peruviana	x			x		
		E. plebeja	x					
		E. vesiculosa						x*
	Erythrodiplax	*E. fervida*	x					x
		E. funerea					x	x
		E. fusca	x	x	x		x	x
		E. umbrata		x*				

Libellula	*L. herculea* cf.	x					
Macrothemis	*M. pseudimitans*		x	x			
Miathyria	*M. Marcella*	x				x	
Micrathyria	*M. aequalis*	x	x	x	x	x	
	M. atra			x			
	M. mengeri					x	
	M. ocellata	x		x			
	M. schumanni				x		
Orthemis	*O. discolor*	x	x		x		
	O. ferruginea		x			x	
Paltothemis	*P. lineatipes*				x		
Pantala	*P. flavescens*					x	
	P. hymenaea					x*	
Perithemis	*P. mooma*	x	x	x		x	x
Tauriphila	*T. australis*					x	
	T. argo	x*					
Tramea	*Tramea* sp.	x*					

*Species observed *in situ*

** Species obtained by rearing

ANOSIM showed significant differences in assemblage composition among all six lakes (Global R = 0.68, $p = 0.001$). Pairwise comparison showed high dissimilarity values among lakes (R >75, Table 5). Ten Odonata taxa were selected as significant species indicators of our lakes (Table 6). IndVal analysis showed that rural sites were those with the highest number of species. Of these, CATIE is the best characterized by 13 species, while El Rodeo is characterized six species, the same as the urban lake La Sabana. The semi-urban sites (Doña Ana and Lankester) were characterized by four and three species, respectively. Lake La Paz, one of the urban sites, has been identified only by an *Enallagma novaehispaniae* species (Table 6).

Table 5. One-way ANOSIM results for pairwise comparisons among six lakes using Odonata abundance data. Name of sites: DA (Doña Ana), ER (El Rodeo), CAT (Catie), LP (La Paz), LS (La Sabana), LAN (Lankester).

Groups compared	***R***	***P***
DA vs ER	98.93	0.0001
CAT vs LP	96.28	0.0001
DA vs LAN	91.97	0.0001
ER vs LP	90.26	0.0001
DA vs LP	90.11	0.0001
LS vs LP	90.06	0.0001
ER vs LS	89.58	0.0001
CAT vs ER	88.72	0.0001
CAT vs DA	85.44	0.0001
CAT vs LAN	83.98	0.0001
LAN vs LP	83.67	0.0001
DA vs LS	83.05	0.0001
LAN vs LS	80.64	0.0001
CAT vs LS	79.12	0.0001
ER vs LAN	78.05	0.0001

Table 6. Indicator value analysis of different groups (Association function: IndVal.g Significance level (alpha): 0.05) in urban lakes (U), semi-urban (SU) and rural (R) of the ce ntral area of Costa Rica.

Group	**Taxon**	**Indicator value**	***p* value**
Catie (R)	*Erythemis attala*	0.949	0.0002
	Telebasis digiticolis	0.949	0.0002
	Telebasis filiola	0.949	0.0002
	Acanthagrion speculum	0.894	0.0002
	Erythemis peruviana	0.882	0.0002
	Erythrodiplax fervida	0.861	0.0002
	Micrathyria aequalis	0.847	0.0002
	Neoerythromma cultellatum	0.846	0.0002
	Eryhrodiplax fusca	0.838	0.0002
	Micrathryria ocellata	0.816	0.0004
	Erythemis plebeja	0.707	0.0004
	Perithemis mooma	0.696	0.0026
	Brachymesia furcate	0.618	0.0066
El Rodeo (R)	*Acanthagrion trilobatum*	1	0.0002
	Argia pulla	0.92	0.0002
	Aphylla sp.	0.791	0.0002
	Orthemis discolor	0.77	0.0004
	Dythemis sterilis	0.531	0.031
	Argia translata	0.5	0.0178
Doña Ana (SU)	*Anax junios*	0.846	< 0.001
	Ischnura ramburii	0.846	< 0.001
	Remartinia luteipennis	0.827	< 0.001
	Ischnura capreola	0.764	< 0.001
Lankester (SU)	*Anisagrion allopterum*	0.856	< 0.001
	Hetaerina cruentata	0.775	< 0.001
	Argia anceps	0.723	< 0.001
La Sabana (U)	*Orthemis ferruginea*	0.837	0.0002
	Pantala flavescens	0.832	0.0002
	Miathyria marcella	0.799	0.0002
	Enallagma civile	0.779	0.0002
	Micrathyria mengeri	0.548	0.0234
	Pantala hymenaea	0.548	0.0232
La Paz (U)	*Enallagma novaehispaniae*	0.671	0.0018

Relationships between Odonata assemblages and environmental parameters CCA

Canonical Correspondence Analysis (CCA) ordination (Fig. 5), showed a significant effect of four physicochemical variables in the Odonata assemblages (χ^2 =0.54, F=2.58, p=0.001). The first two dimensions of CCA have a significant effect: CCA1 (χ^2 = 0.23, F=4.44, p=0.001), CCA2 (χ^2 = 0.15, F=2.82, p= 0.008). We observed four groups formed. The first group is CATIE, positively influenced by temperature and negatively by conductivity, being this variable the one that mainly determines the presence of the species at this site. The second group is formed for El Rodeo, positivity influenced by conductivity and negative influenced by pH. The Lankester is the third group possibly defined by intermediate values of conductivity, dissolved oxygen and pH. The fourth groups was formed by La Paz and Doña Ana, where the assemblages were mostly influenced by dissolved oxygen and pH.

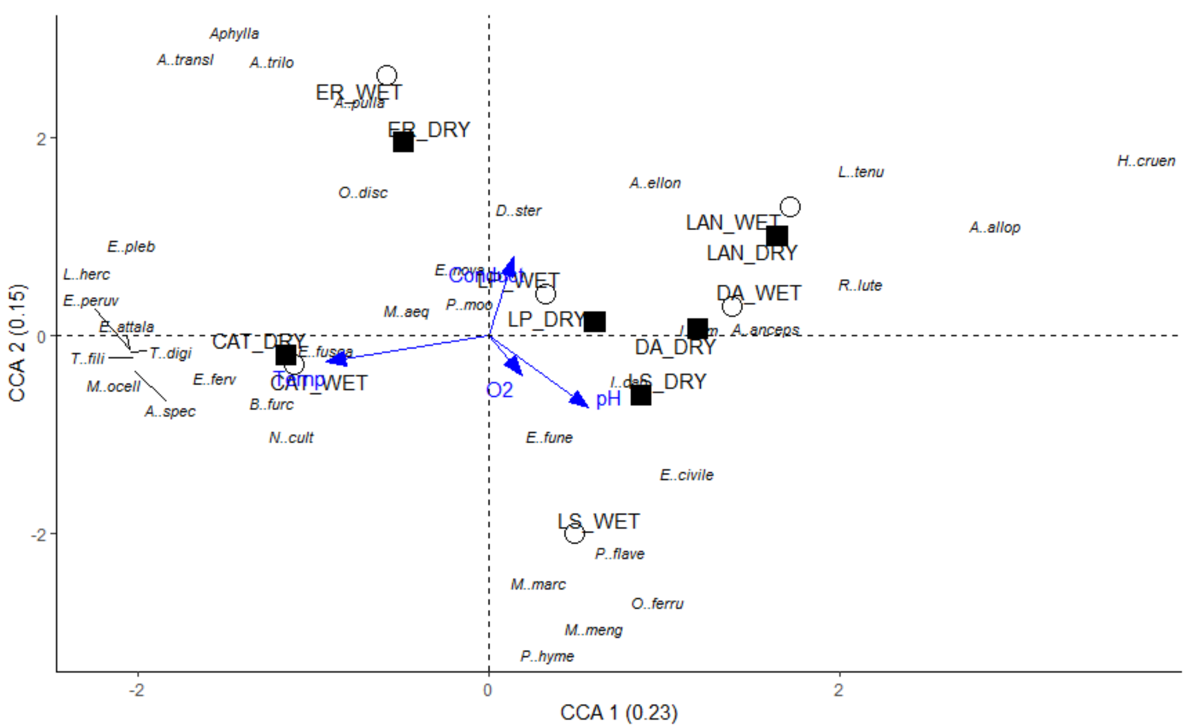

Figure 5. CCA result for relationship between Odonata assemblage and physicochemical variables in sampling sites.

DISCUSSION

Our study identified the first evaluations of adult odonates as bioindicators for lakes in the Central America, with different anthropogenic gradient (rural, semi-rural, urban). Due to their life cycle, odonates in stadium adult can be used for complementary conservation strategies in aquatic and terrestrial ecosystems; they are very conspicuous (Foote & Rice-Hornung 2005, Reece & Mcintyre 2009, Villalobos-Jiménez et al. 2016). Our findings highlight the influence that physicochemical variables and anthropogenic disturbances (effects of urbanization) have on the Odonata and are reflected in the composition and abundance of its populations. We found that rural lakes have a great diversity of dragonflies and, although in less diversity, the urban environments are colonized by species that are being more tolerant to the different stressors that influence these ecosystems. We identified the different species indicating the composition at each of the sites (Table 4a, b); as well as specifically registering those that only inhabit lentic environments. In addition, the following species were found only in urban environments: *Enallagma civile, E. novaehispaniae, Dythemis nigra, Erythemis vesiculosa, Erythrodiplax funerea, Micrathyria mengeri, Pantala flavescens, P. hymenaea, Tauriphila australis.* Species that were recorded only in semi-urban sites were: *Anisagrion allopterum, Argia ellongata, Lestes tenuatus, Remartinia luteipenis* and those exclusively found in rural environments were *Acantagrion* and *Telebasis* species. It should also be considered that some species such as *Enallagma civile, E. novaehispaniae, Neoerythromma cultellatum, Lestes tenuatus, Brachymesia furcata, Miathyria marcella, Micrathyria aequalis, M. atra, M. mengeri, M. ocellata, M. schumanni, Pantala flavescens, P. hymenaea, Tauriphila australis, T. argo, Tramea* sp., reported in this study have been recorded previously only in lentic environments (Ramírez 2010). Our results suggest that urban lentic environments are important spots that can support the conservation of Odonata species.

As expected, we found a strong influence of the physicochemical variables on the Odonata assemblages. However, the pattern was not related to the level of urbanization since the environmental variables did not change in relation to the degree of anthropogenic impact (Fig. 1). The PCA grouped the sites showing the influence of the physicochemical variables, the response coincides with that of other studies where physicochemical variables such as pH, dissolved oxygen, temperature and conductivity influence the evaluated sites, increasing or decreasing the richness or abundance of the organisms that inhabit these environments (Hassall et al. 2010, Hassall 2014, Villalobos-Jiménez 2016). ANOSIM confirmed the significant differences in the composition of the odonate assembly between the study sites. The indicative value showed that the rural lake CATIE is characterized by 13 species and represents the greatest wealth of the all sites, while the lowest wealth was recorded in the urban lake La Paz, with only one characteristic species, *Enallagma novaehispaniae*. We suggest that the difference between the sites is influenced by the physicochemical variables, also by the presence or absence of aquatic vegetation, since although a strict evaluation was not carried out, in models where some variables were eliminated, the vegetation showed influence on the assembly of the odonates. Vegetation is a substrate for larvae and perches for adults, providing microhabitats allowing them to reduce inter and intraspecific competition. It also acts as a refuge from the presence of predators for odonates, such as fish, waterfowl and other aquatic macroinvertebrates (Remsburg et al. 2008, Villalobos-Jiménez et al. 2016, Silva et al. 2010).

Of the families collected, we observed a dominance in Libellulidae and Coenagrionidae, with ~30% and ~23% of the total species for the country, respectively. These families are highly diverse in Costa Rica, with 95 species for Libellulidae and 66 species for Coenagrionidae (Paulson 2020). This agrees with other studies carried out in tropical areas where both families are reported as the most diverse (Altamiranda-Saavedra 2009, Bota-Sierra et al. 2016), as well as an association between urban pollution with the increase in the abundance and dominance of the Libellulidae family (Ferreras-Romero et al. 2009). Our results allow, despite having less diversity, to visualize lentic environments with anthropic influence, since although the negative impact of urban disturbances they harbor species that inhabit only this type of ecosystem (Goertzen & Suhling 2013, Hassall 2014, Perron & Rick 2019).

Of the 51 species collected, only *Ischnura ramburii* is shared among the six lakes studied and four species are shared among five sites: *Ischnura capreola*, *Erythrodiplax fusca*, *Micrathyria aequalis* and *Perithemis mooma*. Other species such as *Argia anceps*, *Neoerythromma cultellatum*, *Dythemis sterilis* and *Orthemis discolor* were registered in the three types of lakes: rural, semi-urban and urban, which indicates that they are species that can adapt to environments with different conditions, the so-called Euritopic species (Garzón-Sanabria & Realpe 2009). Among the species suggested by Garzón-Sanabria & Realpe (2019) as euritopicas are *Acanthagrion trilobatum*, *Brachymesia furcata*, *Dythemis sterilis*, *Erythrodiplax fusca*, *Orthemis discolor*, which were registered in our study and which can be widely dispersed. Furthermore, Gómez-Anaya et al. (2011) suggest that the genera *Orthemis* and *Perithemis* are opportunistic in lentic bodies of water. In other studies, *Erythrodiplax fusca* has been classified as a species that presents tolerance to urban stressors (Villalobos-Jiménez et al. 2016), this species was registered in the two urban sites of our study.

Our data indicates that all the measured variables influence the assembly of dragonflies in different ways, at the sampled sites. Although transparency was not evaluated, the CATIE urban site, which always had the greatest abundance and richness, showed 100% transparency during the sampling days. This behavior has been reflected in other studies where the richness and abundance of odonates is influenced, due to their sensitivity to structural changes, by changes in aquatic and riparian vegetation (eg Samways et al. 1996, Foote & Rice 2005, Vilela et al. 2016, Córdoba-Aguilar & Rocha-Ortega 2019, Juen & Feest 2019, Palacino-Rodríguez et al. 2020). The presence of vegetation provides resources, both microhabitats, availability of food since it is a refuge for other organisms, while they function as perches for adults. This will favor the protection of their territory, as well as the benefit to assist in their thermoregulation and surveillance of the dams from their perch sites, increasing their alpha diversity (Remsburg et al. 2008, Goertzen & Suhling 2013, Orejuela-Yustes 2017, Perron & Rick 2019). Having a greater availability of microhabitats can reduce both food competition, as well as decrease predation and with this increase the abundance of organisms.

The results of our study show a high importance of the preservation of urban aquatic sites and that populations of different native aquatic plants may support the conservation of species. Although it was not statistically analyzed, we found greater abundance and richness in sites where the diversity of aquatic plants was greater. This agrees with other studies where the positive relationship between aquatic plants and the abundance and richness of organisms was demonstrated (McKinney 2008, Silva et al. 2010, Goertzen & Suhling 2013, Jeanmougin et al. 2014, Dutra & De Marco 2015, Oliveira-Junior et al. 2015, Vilela et al. 2016, Villalobos-Jiménez et al. 2016, Cuevas-Yáñez et al. 2017, Briggs et al. 2019, Córdoba-Aguilar & Rocha-Ortega 2019).

Odonata richness in our study sites found ~20% of all the species reported for the country, with 51 species. These results were higher compared to other diversity studies in lentic environments in other tropical and European countries, where the observed richness fluctuates between 20 and 40 species (Sahlén & Ekestubbe 2001, Gil Palacio et al. 2007, Orejuela-Yustes 2017). Despite the number of species recorded in our study, research conducted at urban sites shows that odonate diversity is negatively affected by the effects of urbanization (McKinney 2008). While research carried out in countries such as Austria, Germania, France and South Africa shows that vegetation is associated with increased odonate richness in urban lakes (Chovanec et al. 2001, Goertzen & Suhling 2013, Jeanmougin et al. 2014, Samways & Steytler 1996, Vilela et al. 2016). Therefore, a more integrative management of the studied sites and urban areas in general is suggested, implementing measures that allow the introduction of native aquatic plants, in a controlled manner, that help increase the abundance and richness of odonates together with other native aquatic and terrestrial fauna, as part of a more sustainable urban development.

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ARTÍCULO 2

Román-Heracleo, J., M. Springer & R. Novelo-Gutiérrez. (2019). Descriptions of the larvae of *Acanthagrion speculum* and *A. trilobatum* from Costa Rica (Odonata: Coenagrionidae). *Zootaxa* 4624 (2): 219–229.

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Descriptions of the larvae of *Acanthagrion speculum* and *A. trilobatum* from Costa Rica (Odonata: Coenagrionidae)

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Abstract

Description of the final instar of *Acanthagrion trilobatum* Leonard, 1977 and *A. speculum* Garrison, 1985 is based on associated specimens from San José, Turrialba and Sarapiqui Provinces, Costa Rica. Illustrations of these two species and a comparative table summarizing the main features of all larvae of *Acanthagrion* described to date are provided. The larva of *A. trilobatum* is distinguished from that of *A. speculum* by shorter lateral caudal lamellae (length 7 mm vs. 8.2 mm), lateral carina of abdominal segments 2–8 with spiniform setae on posterior 1/3 (lateral carinae of only S6–8 with spiniform setae in *A. speculum*), and male gonapophyses incurved (straight in *A. speculum*).

Key words: Neotropical Region, Zygoptera, damselflies, *Acanthagrion*, taxonomy

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Key words: Neotropical Region, Zygoptera, damselflies, *Acanthagrion*, taxonomy

Resumen

Se hizo la descripción de las larvas de último estadio de *Acanthagrion trilobatum* y *A. speculum* con base en especímenes asociados provenientes de las Provincias de San José, Turrialba y Sarapiquí, en Costa Rica. Se proporcionan ilustraciones y un cuadro que resume las características principales de todas las larvas de *Acanthagrion* descritas a la fecha. La

larva de *A. trilobatum* se distingue de la de *A. speculum* por tener las lamelas caudales laterales más cortas (longitud 7 mm vs. 8.2 mm), la carina lateral de los segmentos abdominales 2–8 con sedas espiniformes en el 1/3 posterior (solo las carinas laterales de S6–8 con sedas espiniformes en *A. speculum*), y las gonapófisis del macho incurvadas (rectas en *A. speculum*).

Palabras clave: Región Neotropical, Zygoptera, libélulas, *Acanthagrion*, taxonomía

Introduction

The genus *Acanthagrion* Selys, 1876 is a common Neotropical genus of Coenagrionidae composed of 45 species (Lozano *et al.* 2017, Lozano & Rodrigues 2018); the genus is distributed from Texas to Central Argentina (Garrison *et al.* 2010). To date, the final instar larvae of 13 species (<30%) has been described (see Table 1). In Middle America, five species of *Acanthagrion* are known: *A. inexpectum* Leonard, 1977, *A. kennedii* Williamson, 1916, *A. quadratum* Selys, 1876, *A. speculum* Garrison, 1985, and *A. trilobatum* Leonard, 1977, of which only the larva of *A. quadratum* has been described (Novelo-Gutiérrez 2009). Of these species, *A. inexpectum, A. speculum* and *A. trilobatum* have been recorded from Costa Rica (Esquivel 2006). In this paper we provide the larval descriptions of two additional species of *Acanthagrion*: *A. trilobatum*, distributed from Honduras to northern South America, and *A. speculum,* which has been reported from Nicaragua and Costa Rica. Descriptions include images of the complete larva and details of morphology to differentiate them from each other as well as from other *Acanthagrion* species.

Material and methods

Mature larvae were collected with an aquatic net and transported to the laboratory for rearing. Emerged adults were maintained alive for a few days and preserved after death in 95% ethanol, together with their exuviae. Additional preserved larvae (in 95% ethanol) were examined. Descriptions and measurements (in mm) were made using a Nikon SMZ 745 stereomicroscope with a calibrated ocular micrometer. Photographs of morphology were taken with a Nikon SMZ25 stereomicroscope and its mounted Nikon DS-U3 camera and processed with the program NIS elements AR version 4.5. Mandible nomenclature follows Watson (1956) and labium nomenclature follows Corbet (1953). Abbreviations are as follows: AL, abdomen length (without caudal lamella); Pfl: prothoracic femur length; MsfL, mesothoracic femur length; MtfL, metathoracic femur length; CeL, cerci length; MgL, male gonapophyses length; FgL, female gonapophyses length; MWh, maximum width of head; TL, total length (including caudal lamellae); S1–10, abdominal segments; F-0, ultimate instar; CATIE (Centro Agronómico Tropical de Investigación y Enseñanza); MZUCR, Museo de Zoología, Universidad de Costa Rica; IEXA, Colección Entomológica "Miguel Angel Morón Ríos" del Instituto de Ecología, A.C.

Results

Acanthagrion trilobatum Leonard, 1977

Figs. 1a, 2b, d, 3c, e–f, 4a, c, 5a–b, 6a–b, 7

Specimens examined. Two exuviae (1♂, 1♀ both emerged), seven F-0 larvae (3♂♂, 4♀♀). **COSTA RICA: San José**, Ciudad Colón, El Rodeo (9.9219°, -84.2552°), elevation 746 m, 07 September 2018, J. Román-Heracleo leg., 2 F-0 larvae (emerged on 10-Sep-2018, 1♀, 12-Sep-2018, 1♂); same data but 5 F-0 larvae (3♂♂, 2♀♀), 24 October 2018, and 2 F-0 larvae (♀♀), 16 January 2019. Three larvae deposited at IEXA; all other specimens in MZUCR.

Description. Exuviae light brown to brown, mature larvae mostly yellowish-brown; slender; femora banded; caudal lamellae very long, 65% of total body length (Fig. 1a).

Head. Subpentagonal, almost twice as wide as long, wider than thorax and abdomen (Fig. 1a). Labrum with ventral margin concave at middle and scattered setae on surface; clypeus mostly glabrous with some long and short delicate setae; frons and vertex flat, mostly glabrous with some scattered long setae. Occipital margin widely concave, straight at middle; cephalic lobes bulging and rounded, with abundant, short, stout spines (as Fig. 2a). Antenna (Fig. 2b) long and filiform, 7-segmented, scape and pedicel brown, cylindrical, flagellomeres elongated, 3rd antennomere longest and uniformly yellowish-brown, antennomeres 4–6 with the basal half light brown, the distal half yellow pale, 7th antennomere pale yellow, proportional lengths of antennomeres: 0.50, 0.70, 1.0, 0.85, 0.50, 0.30, 0.20. Compound eyes moderately developed, wider than long, laterally prominent. Mandibles (as Fig. 3a) with formula R 1+2345 y a / L 1+2345 0 a b, b>a. Maxilla: Galeolacinia with six teeth, three dorsal teeth slightly incurved, similar length and robustness, with a basal row of long thin setae, three ventral teeth of different size and robustness (as in Fig. 3b), size proportions: apical tooth 1.0, median one 0.50, basal tooth 0.15, with a row of setae on ventral side and a basal row of strong, stiff setae which increase in size and robustness apically; maxillary palp gently incurved, ending in a stout, round-tipped spine, with long setae on the external surface. Ventral pad of hypopharynx subpentagonal, anterior margin convex, anterior half with large setae, distal half glabrous. Prementum-postmentum articulation reaching posterior margin of prothoracic coxae; prementum longer than wide (Fig. 3c), sub-rhomboidal, lateral margins slightly concave, widely divergent apically, laterodorsally with a row of eight spiniform setae and a group of three very tiny basidorsal spiniform setae; ligula with tip prominent, widely rounded, finely serrulate, with a minute sub-marginal spine on each side of midline; 2 long premental setae to each side of midline, rarely 2+1, on one side only. Labial palp (Figs. 3c, e) with 4 long setae, apical lobe (Fig. 3e) divided into a squarely truncate dorsal branch composed of four small teeth, the ventral three more or less of same size and robustness, dorsal tooth widest, obtuse and with minute denticles on distal margin, and a ventral branch with a well-developed end hook; ventral margin of palp finely serrate; movable hook almost half the length of labial palp, sharply pointed; two spines at base of palpal articulation. One specimen with a remarkable teratology, in which the prementum has the ligula divided into two lobes and with only 3 palpal setae (Fig. 3f).

Figure 1. Dorsal habitus of the larvae of: a) *A. trilobatum*; b) *A. speculum*.

Thorax. Pronotum light yellowish-brown, subtrapezoidal, posterolateral margin slightly angulated, serrate with the most lateral spiniform setae the longest; posterior margin straight at median. Synthorax yellow dorsally, yellowish-brown laterally; anterior and posterior wing sheaths reaching anterior margin and basal third of S4, respectively.

Legs long (when fully extended, tip of metathoracic tarsi reaching S10), slender, pale with subapical bands on femora; dorsal and ventral borders of femora with a row of spiniform setae, an external row of spiniform seta only on prothoracic femora (Fig. 1a). Tibiae spiny on internal surface, external surface with long delicate setae, apical internal third with abundant tridentate setae (Fig. 4). Tarsi with two ventral rows of spiniform setae, claws simple, with pulvilliform empodium.

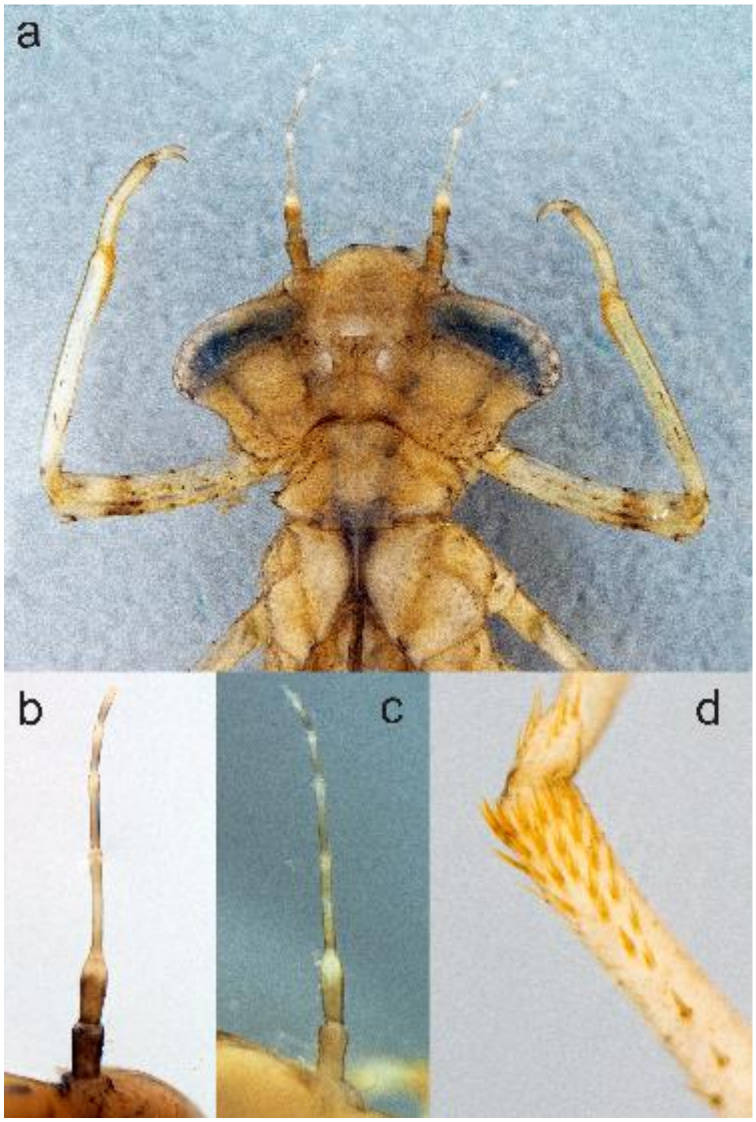

Figure 2. Morphological details of the larvae. Figs. a and c, *A. speculum*; b and d, *A. trilobatum*. a) Head, dorsal view; b) Right antenna, dorsal view; c) Left antenna, dorsal view; d) Distal apex of metatibiae showing tridentate setae.

Abdomen. Light brown (Fig. 1a); S2–9 with a thin pale middorsal line gradually widening on S8–9, a narrow, reddish brown stripe on each side of pale middorsal line. S1–

10 gradually narrowing posteriorly, S2–8 with a lateral carina which bears a row of spiniform setae, increasing in number and robustness posteriorly, S9–10 without such carina but with a row of spiniform setae. Dorsal surface of S5–10 with spiniform setae which increase in abundance and robustness caudally, and a transversal, subapical row of spiniform setae which increase in robustness on posterior segments (Fig. 1a). Sterna 1–6 lacking spiniform setae, sterna 7–10 with spiniform setae, increasing in abundance and robustness caudally. Posterior margin of sterna 1–9 smooth, that on 10 with a row of stout spiniform setae. Male gonapophyses (Fig. 4a) long, surpassing well beyond the posterior margin of sternite 9, slightly incurved in ventral view, sharply pointed, ventral border with a row of five spines and a long seta at the base of each spine. Female gonapophyses (Fig. 4c) surpassing well beyond the posterior margin of sternite 10, external valve longer than internal ones, ventral border with a row of five spines and a long seta at the base of each spine; external valve sharply pointed, internal valve roundly tipped. Caudal lamellae (Figs. 5a–b) membranous with visible tracheae, lanceolate, seven times longer than their widest part, mostly translucid, creamy pale basally, ending in a short, sharply pointed tip, without filament, measuring 41.1–44.7% of total body length, with a row of spines on lateral carina; nodus approximately at midlength in median and lateral lamellae; basal half of dorsal margin of median lamella with 26 small spines, basal 0.25 of ventral margin with 10 minute spines (Fig. 5a); basal 0.25 of dorsal margin of lateral lamellae with nine minute spines, basal 0.54 of ventral margin with 41 small spines (Fig. 5b), remainder of margins in both median and lateral lamellae with a row of minute and very fine setae. Cerci slightly longer than wide, widely round-tipped in male (Fig. 6a), conical in female (Fig. 6b).

Measurements (mm): Larvae only: TL 17–19; AL 7–8.5; PfL 1.8─2; MsfL 2.4─2.5; MtfL 3; MWh 2.8; CeL 0.2; MgL 0.5; FgL 0.9. Lateral lamella length 7–7.5, maximum width 1.0. Largest measurements correspond to males.

Remarks. The recreational park El Rodeo is located to the west of the Central Valley of Costa Rica. It stands out for being the greatest fragment of forest in this area of the country. It is located within the forest reserve of the University for Peace. A description of the physical characteristics is provided in Cascante-Marín (2012). The samples were collected in an artificial lake lacking aquatic vegetation that is filled with rainwater (Fig. 7); for this reason, there is variation in depth throughout the year. The lake has a heterogeneous margin consisting of an abrupt edge on one side, while the rest is beach; the border is surrounded mostly by grasses (Poaceae). The larvae were found into the sediments. Larvae were collected during the months of August to January, with the highest emergence activity in September. The highest incidence of adult activity was observed during September to December.

Acanthagrion speculum Garrison, 1985

Figs. 1b, 2a, c, 3a–b, d, 4b, d, 5c–d, 6c, 8

Specimens examined. Six exuviae (1♂, 5♀♀), eight F-0 larvae (4♂♂, 4♀♀). COSTA RICA: Turrialba, CATIE (9.8906°, –83.6545°), elevation 611m, 1 F-0 larva (♀ reared), 09 May 2018, J. Román-Heracleo leg., emerged on 16 May 2018; same data but 3 ♀♀ emerging, 22 August 2018; same data but 2 F-0 larvae 24 Sep 2018 (1♂ reared, emerged on 25 Sep 2018, 1♀ reared emerged on 29 Sep 2018); same data but 5 F-0 larvae (3♂♂, 2♀♀), 21 November 2018; same data but 3 F-0 larvae (1♂, 2♀♀), 19 January 2019. Sarapiquí, Reserva Biológica Tirimbina, lake (10.4238°, –84.1051°) elevation 163m, 2 F-0 larvae (♂♂), 27 October 2018, (1♂ emerged 29 October 2018, 1♂ died), P. E. Gutiérrez-Fonseca, J. Román-Heracleo, leg. Specimens deposited at IEXA (4 larvae), all other in MZUCR.

Description. Exuviae yellowish, mature larvae mostly yellowish-brown, slender, femora with preapical bands, caudal lamellae 80% of total body length (Fig. 1b). Larvae similar to *A. trilobatum* described above, except as follows:

Head. Antennomeres (Figs. 2a, c) 2–6 brown with apex yellow pale, 7th antennomere yellow pale, size proportions of antennomeres: 0.50, 0.70, 1.0, 0.70, 0.50, 0.40, 0.10 (Fig. 2c). Prementum with 3 long setae, occasionally 2+1 (Fig. 3d), laterodorsally with a row of 6–9 spiniform setae. Labial palp with 3–4 long setae, usually 4 (Fig. 3d).

Thorax. Anterior and posterior wing sheaths reaching posterior margin of S4 and basal third of S5, respectively (Fig. 1b). Metathoracic legs long, when fully extended tips of tarsi reaching posterior margin of S8.

Abdomen. S1–9 with a thin pale middorsal line, S2–8 with a prominent lateral carina, S6–9 with lateral spines at posterior third of each segment, increasing in number (2–4 or 5 spines) and robustness caudad (Fig. 1b). Male gonapophyses, in ventral view (Fig. 4b) straight, sharply pointed, reaching basal 0.56 of sternum 10. Ventral view of female gonapophyses as in Fig. 4d. Caudal lamellae (Figs. 5c,d) eight times longer than widest part, measuring 44.6–45.5% of total body length; nodus inconspicuous, delimited by the lateral carina and the row of spines on the ventral margin of lateral lamellae; basal 0.7 of dorsal margin of lateral lamellae with two spines, basal 0.52 of ventral margin with 34 spines (Fig. 5d); basal 0.10 of dorsal margin of median lamella with two spines, basal 0.05 of ventral margin with two spines (Fig. 5c); remainder of margins in both median and lateral lamellae with a row of minute and very fine setae. Male cerci more or less as wide as long, conical, blunt-tipped (Fig. 6c).

Measurements (mm): Larvae only: TL 17.7–18; AL 7.6–8.2; PfL 1.9–2.0; MsfL 2.3–2.5; MtfL 3; MWh 2.8; CeL: 0.2; MgL 0.5 (Figure 5b); FgL 1.0 (Figure 5d). Lateral lamella length 7.9–8.2, maximum width 1.0. The largest measurements correspond to males.

Remarks. The CATIE is located on the Caribbean slope, in Turrialba, Costa Rica. Its lake (Fig. 8a) is man-made with influence of the surrounding agroforestry land. The aquatic vegetation is represented mostly by *Nymphaea* spp. and *Eichhornia* sp., and grasses of the Poaceae family on the shore. Larvae were collected from February 2018 to January 2019, associated with the roots below the leaves of the aquatic plants (water lily mainly), although the larvae found at the Tirimbina Lake (Fig. 8b) were found on muddy substrate. Adults emerged throughout the year, however, the highest emergence activity was during May (females) and September (males). Metamorphosis occurred 3─15 cm above the water surface, on vegetation.

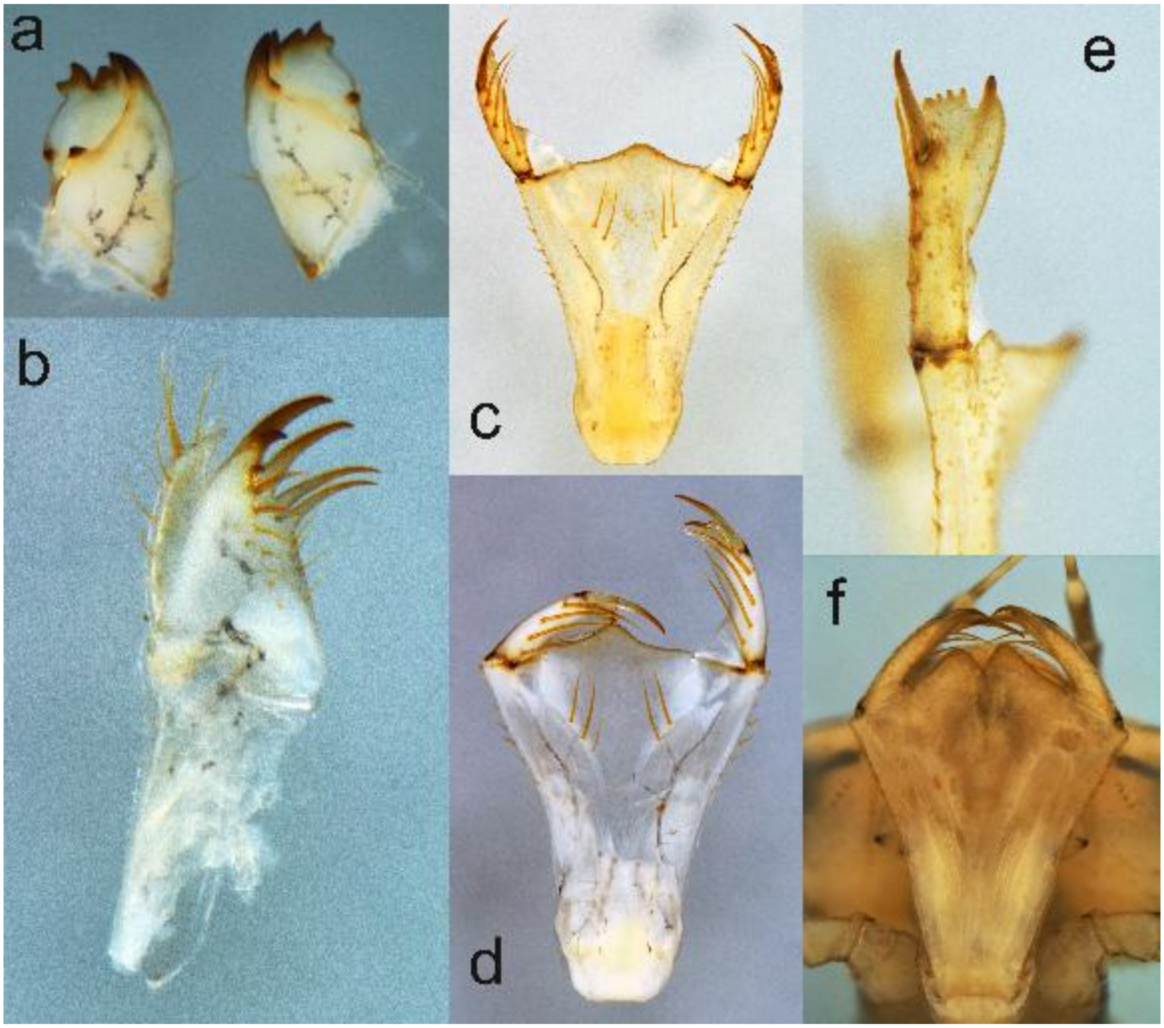

Figure 3. Morphological details of the larvae. Figs. a, b and d, *A. speculum;* c, e and f, *A. trilobatum*. a) Mandibles, ventrointernal view; b) Right galeolacinia, ventral view; c) and d) Prementa, dorsal view; e) Right labial palp, anterior view; f) Prementum teratology, ventral view, showing bilobate ligula.

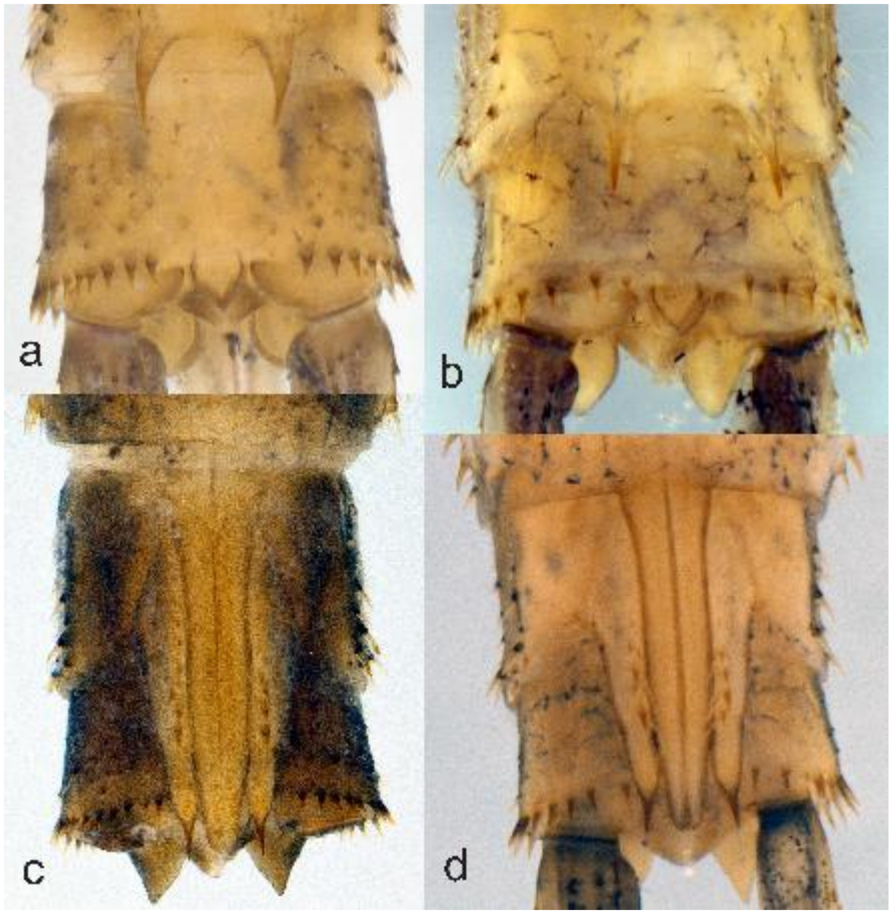

Figure 4. Morphological details of the abdominal segments 9–10 of the larvae. Figs. a and c, *A. trilobatum*; b and d, *A. speculum*. a–b, Male gonapophyses, ventral view, c–d, Female gonapophyses, ventral view.

Diagnosis. *Acanthagrion trilobatum* differed from *A. speculum* (characteristics of the latter in parentheses) by having 2–3 premental setae, rarely 3 (2 large +1 smaller or 3, usually 3); antennomere length proportions, especially 4th antennomere 0.85 times the length of the 3rd antennomere (0.70); labial palp with 4 long setae (3─4, usually 4); S2–8 with lateral carina and spiniform setae (S2–8 with lateral carina, but only S6– 9 with spiniform setae); male gonapophyses slightly incurved (straight); male cerci widely rounded at apex (bluntly-pointed); caudal lamella 41.1–44.7% of body length (44.6–45.5%); tracheal pattern appearing with incipient, dark, transversal bands, secondary trachea diffuse (tracheal pattern lighter, no faint of any transversal band especially in lateral lamellae, secondary trachea well-marked).

Table 1. Larval characters for species of *Acanthagrion.* Modified from Anjos-Santos *et al*. (2011). L = length; number of palpal setae and premental setae is for one side.

Species	Described by	Total L	Cephalic lobes	Number of antenomeres	Palpal setae	Premental setae	Wing pads reaching**	Apex of caudal lamellae	Nodus/lamella length***	Groups *sensu* Novelo-Gutierrez 2009
A. adustum	Geijskes 1943	11.5–13.0	strongly angulated	6	4	1	anterior margin of S5	nearly rounded	0.55	I
A. aepiolum	Lozano et al., 2007	9.8–11.0	rounded	6 or 7	4	2+1~	middle of S4	acute, almost rounded	0.60	II
A. apicale	De Marmels 1992	10.5	rounded	7	4	2+1	base of S5	acute	0.53	II
A. ascendens	Geijskes 1941	15–17 *	rounded	7	4	2+1	middle of S5	acute	0.48	II
A. floridense	Lozano et al., 2017	9.8–11.0	rounded	7	4	3	half of S4	acute	0.55	II
A. fluviatile	De Marmels, 1990	9.5–10.5	strongly angulated	6	4	1	S4 in female, S5 in male	nearly rounded	0.58	I
A. gracile	Anjos-Santos et al., 2011	10.4–12.8	rounded	7	4	3 or 3+1	middle of S4	acute	0.50	II
A. hildegarda	Muzón et al., 2001	8	rounded	7	5	3	S4	acute	beyond basal 0.50	II
A. indefensum	Geijskes, 1943	10	strongly angulated	6	4	1	S5	nearly rounded	0.57	I
A. lancea	Anjos-Santos et al., 2011	9.8–10.9	rounded	7	4	2+1 or 3	middle S4	acute	0.60	II
A. quadratum	Novelo-Gutiérrez, 2009	9.8–13.9	rounded	7	4	3	S5	acuminate	0.53	II

A. speculum		9.8–10	bulging and gently rounded	7	3 or 4, usually 4	2+1 or 3	posterior margin S4 and basal third of S5	nearly rounded	0.55	II
A. trilobatum		10–11.5	bulging and gently rounded	7	4	2+1	basal third of S4	short sharply pointed	0.54	II
A. vidua Selys	De Marmels, 2007	9.3–10.5	rounded	7	4	2 or 1+1	middle of S4	acute	0.42	II
A. viridescens	Gutiérrez et al., 2015	12.4	rounded	7	4	3	S4	acute	0.60	II

* Lamella length included

** Instar F-0, with abdomen not distended

*** This metric refers to the position of the nodus in relation to the total length of a lateral caudal lamella measured along the dorsal margin

~ The number after the + sign means a smaller seta

Figure 5. Caudal lamellae, left lateral view: a,c, Median lamella; b,d, Lateral lamella . a–b, *A. trilobatum*; c–d, *A. speculum*.

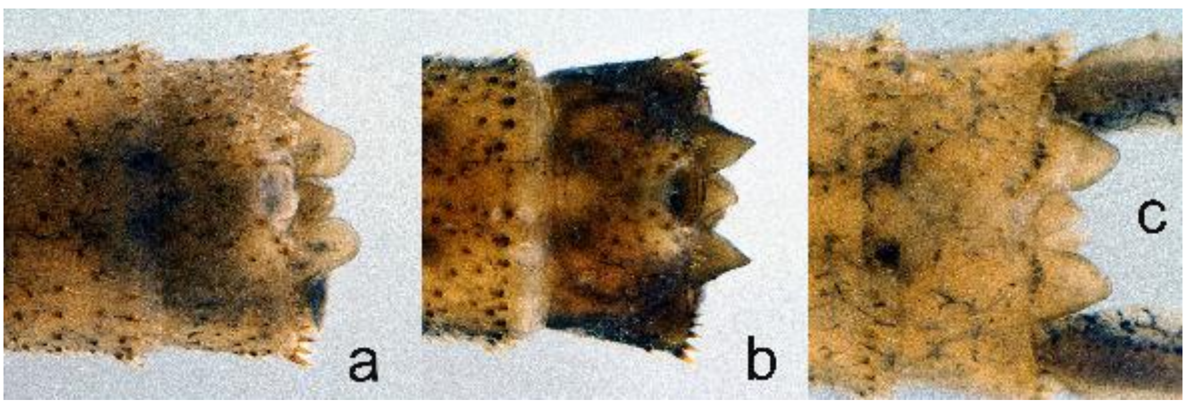

Figure 6. Cerci, dorsal view: a–b) male and female of *A. trilobatum*, respectively; c) male of *A. speculum*.

Discussion

The known *Acanthagrion* larvae are morphologically very similar. Based upon the two groups proposed by Novelo-Gutiérrez (2009), Anjos-Santos et al. (2011) provided a table with features to distinguish such groups of *Acanthagrion* larvae, including the larvae of *A. gracile* and *A. lancea* described by them. They addressed the larvae of *A. hildegarda* and *A. quadratum*, left undefined by Novelo-Gutiérrez (2009), into group II. Lozano et al. (2017), in their description of the larva of *A. floridense*, considered this species belonging to group II. Here, we consider *A. trilobatum* and *A. speculum* belonging to group II as well, sharing characteristics of antenna 7-segmented, usually 4 palpal setae, and 2+1 or 3 premental setae. Table I summarizes characteristics for all known larvae. As can be seen in this Table, the shape of cephalic lobes, the number of antennomeres and premental setae, and the position of nodus in relation to the total length, appear as the most useful characteristics for the separation of species in the genus, while total body length, shape of caudal lamellae apices and number of palpal setae appear to be of minimal value.

FigureS 7–8. Figure 7. Lake El Rodeo, San José, Costa Rica. Habitat of *Acanthagrion trilobatum*. Figure 8. Habitat of *Acanthagrion speculum*: a) Lake CATIE, Turrialba, Costa Rica; b) La Tirimbina, Sarapiquí, Costa Rica.

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ARTÍCULO 3

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Description of the final stadium larva of *Anisagrion allopterum* (Odonata: Coenagrionidae)

Jareth Román-Heracleo & Rodolfo Novelo-Gutiérrez

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Description of the final stadium larva of *Anisagrion allopterum* (Odonata: Coenagrionidae)

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Abstract

The final stadium larva of *Anisagrion allopterum* is described for the first time for Middle America, based upon specimens reared and emerging in the field, from Cartago, Province, Costa Rica. Detailed illustrations are also provided. The larva of this species is characterized by a slender yellow body, premental setae 4+1, five palpal setae, male cerci globose, and caudal lamellae densely tracheate.

Keywords: Neotropical Region; Costa Rica; Zygoptera; reared specimens; taxonomy; damselfly; dragonfly

Introduction

Anisagrion is a small genus of Neotropical damselflies distributed from southern Mexico to northern South America (Colombia, Venezuela and Ecuador) (Garrison, von Ellenrieder, & Louton, 2010; Rojas-Riaño, 2011). In Middle America it is represented by only three species: *Anisagrion allopterum* (Selys, 1876), *A. kennedyi* Leonard, 1937, and *A. truncatipenne* Calvert, 1902. To date, the only larva known of the genus is that of *A. inornatum* (Selys, 1876), described by Tennessen (2012), the only species recorded for South America. In this paper, we provide the description of the last stadium larva of *A. allopterum* based upon four exuviae (reared), and three F-0 larvae. This represents the first larval description of *Anisagrion* for Middle America.

Methods

Mature larvae were collected with an aquatic net and transported to the laboratory for rearing. Emerged adults were maintained alive for a few days and preserved after death in 95% ethanol, together with their exuviae. Additional larvae preserved in ethanol 96% were also examined. The descriptions and measurements (in mm) were made using a Nikon SMZ745 stereomicroscope with a calibrated ocular micrometer. Photographs of morphology were taken with a Nikon SMZ25 stereomicroscope (Chiyoda-ku, Tokyo, Japan) and its mounted Nikon DS-U3 camera, and processed with the program NIS elements AR version 4.5 (Laboratory Imaging s.r.o, Praha, Czech Republic). Mandible nomenclature follows Watson (1956) and labium nomenclature follows Corbet (1953). Abbreviations are as follows: AL, abdomen length (without caudal lamella); FfL, fore femur length; HfL, hind femur length; MfL, medium femur length; Ce, cerci; MgL, male gonapophyses length; FgL, female gonapophyses length; MWh, maximum width of head; TL, total length (including caudal lamellae); S1–S10, abdominal segments; F-0, ultimate stadium; Ep, epiproct; Pp, paraproct; MZUCR, Museo de Zoología, Universidad de Costa Rica; IEXA, Colección Entomológica “Miguel Angel Morón Ríos” del Instituto de Ecología, A.C. Specimens are deposited in MZUCR and IEXA.

Results

Final stadium larva of *Anisagrion allopterum*

(Figures 1–6)

Specimens examined

Four exuviae (3♀, 1♂, emerged), 3 F-0 larvae (2♀, 1♂). COSTA RICA: Cartago; Paraíso, Jardín Botánico Lankester (9.84011 N; 83.88931 W; elevation 1369 m); 23 February 2018 (2♀, emerging in the field); 15 March 2018 (1♂, emerged 16 March 2018); 13 April 2018 (2♀, one emerged 30 April 2018, the second one emerged 1 May 2018); 25 September 2018 (1♂). Laguna Doña Ana (9.83291 N; 83.87810 W; elevation 1345 m); 9 April 2018 (1♀, reared, no data of emergence available), all J. Román-Heracleo leg. Specimens deposited at IEXA (two larvae), all other in MZUCR.

Description

Exuviae and mature larvae mostly yellowish, slender, femora slightly banded, caudal lamellae markedly tracheate (Figure 1).

Figure 1. *Anisagrion allopterum*, female. Habitus dorsal of the F-0 larva.

Head. Subpentagonal, almost twice as wide as long, wider than thorax and abdomen (Figure 1). Labrum ventral margin concave at middle, with scattered setae on surface; clypeus mostly glabrous; frons and vertex flat; minute granules on vertex close to compound eyes internal margin. Occipital margin (Figure 2a) widely concave; cephalic lobes rounded, with stout spiniform setae. Antennae (Figure 2b) filiform, 7-segmented, scape and pedicel cylindrical, with a lateral, longitudinal, brown stripe to each side, flagellomeres elongated, 3rd antennomere the longest, antennomeres 3–6 uniformly yellowish, basal half of 7th antennomere light yellowish brown, the distal half translucid, size proportions of antennomeres: 0.40, 0.70, 1.0, 0.60, 0.40, 0.40, 0.20. Compound eyes moderately developed, wider than long, laterally prominent. Mandibles (Figure 2c) with formula: R 1+2345 y a / L 1+2345 0 a b, b>a. Maxilla's galeolacinia (Figure 2d) with six teeth, three dorsal teeth slightly incurved, similar length and robustness, with a basal row of seven long thin setae, three ventral teeth of different size and robustness, size proportions: apical tooth 1.0, median one 0.55, basal tooth a mere spine, with a basal row of strong stiff setae which increase suddenly in size and robustness apically, maxillary palp gently incurved, ending in a stout spine, with long setae on the external surface. Ventral pad of hypopharynx subpentagonal, anterior margin convex, basal half with large setae, distal half glabrous, three setae on each anterolateral corner. Labium: Prementum–postmentum articulation reaching mesocoxae; prementum (Figure 2e) longer than wide, subrhomboidal, lateral margins slightly concave, widely divergent apically, laterodorsal margin with a row of seven, rarely 6, 8 or 9 spiniform setae and a group of three very tiny basidorsal spiniform setae, forming a triangle; ligula with tip prominent, convex, finely serrulated, with a minute submarginal spine two each side of midline; 4+1 long premental setae to each side of midline, rarely 3+1. Labial palp (Figure 2e, f) creamy pale with a dorsoexternal, longitudinal, darker stripe (Figure 2f), with five long setae, rarely six, its apical lobe (Figure 2f) divided into a squarely truncate dorsal branch which has the distal margin with three small inferior teeth more or less of the same size and robustness, and 4–5 superior minute denticles, and a ventral branch with a well-developed end hook, slightly down curved; internal margin of palp finely serrate; movable hook scarcely more than half the length of labial palp, sharply pointed.

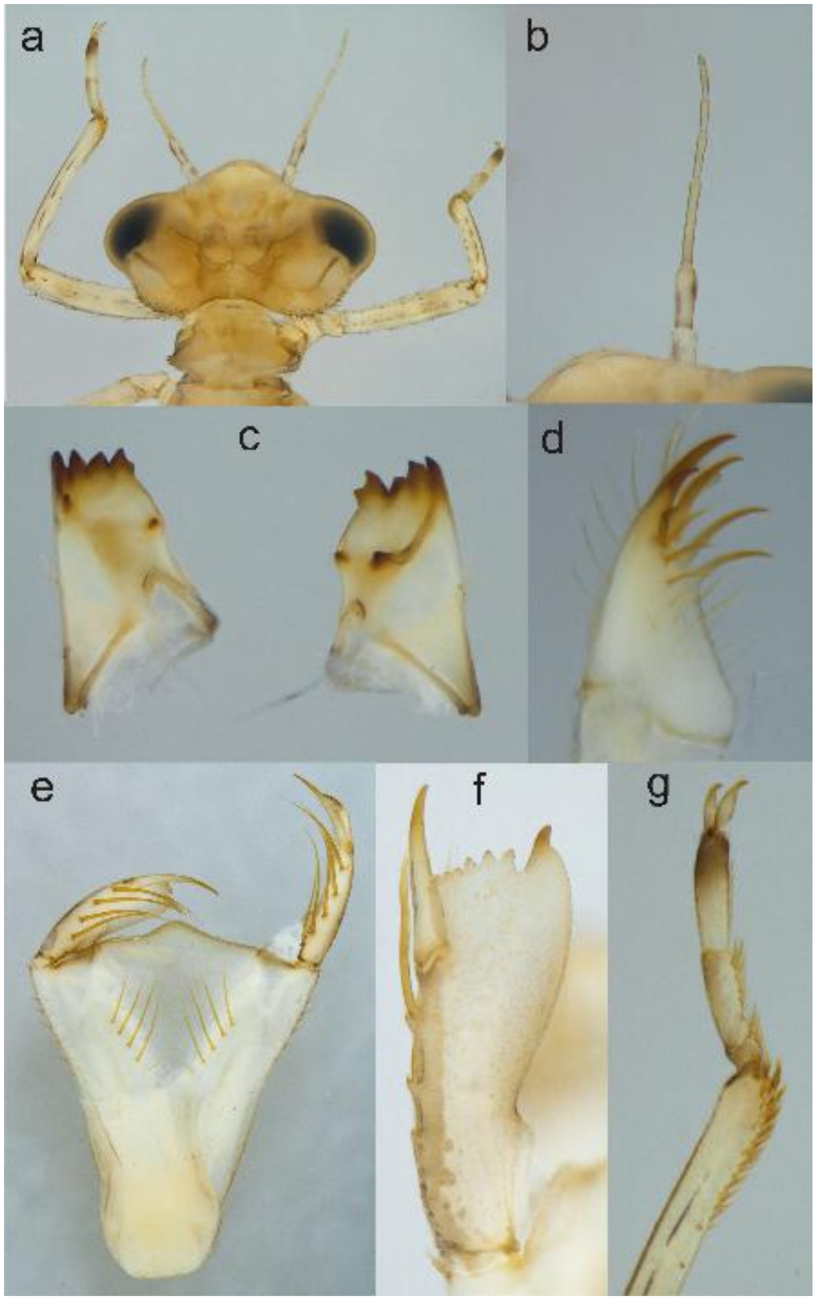

Figure 2. *A. allopterum* details of larval morphology. (a) Head of male, dorsal view; (b) right antenna, dorsal view; (c) mandibles, ventrointernal view; (d) right galeolacinia, ventral view; (e) dorsal view of prementum showing premental setae, laterodorsal spiniform setae, and palp setae; (f) labial palp, anterior view; (g) distal end of tibia and tarsomeres of foreleg, dorsolateral view.

Thorax. Pronotum (Figure 2a) yellowish-brown, subtrapezoidal, posterolateral margin angled, brown, serrate, with 7–9 lateral, small, spiniform setae, posterior margin as shown in Figures 1 and 2a. Synthorax yellow dorsally, yellowish-brown laterally; anterior and posterior wing sheaths reaching the distal third of S4 (Figure 1). Legs long (e.g. when fully extended, hind legs reaching posterior margin of S10, articulation of hind femur reaching posterior margin of S4), slender, yellow pale, with a thin, dorsal, longitudinal brown stripe on femora and tibiae. Femora with a subapical, diffuse band, a dorsal, longitudinal carina on fore- and middle femora, hind femora double-carinated, dorsal and ventral borders with a row of spiniform setae (Figure 1). Tibiae spiny on ventral (internal) surfaces, dorsal (external) surfaces with long delicate setae, apicointernal third with abundant tridentate setae (Figure 2 g). Tarsi with two ventral rows of spiniform setae, basal tarsomere light brown, distal tarsomere with basal half yellow, distal half dark brown (Figure 2 g), all tarsi with long and delicate setae on dorsal surface, claws simple, with pulvilliform empodium.

Abdomen. S1 –1 0 yellowish (Figure 1), S2–8 with a thin, pale, middorsal line, S5 –9 with a reddish-brown, subrectangular spot to each side of pale middorsal line which reduces in length gradually on posterior segments. S1–10 gradually narrowing posteriorly, dorsal surface of S5–10 with spiniform setae which increase in abundance and robustness caudad, S7–10 with a transversal, subapical row of spiniform setae which increase in robustness caudad; posterior margin of S10 with 3–6 stout enlarged setae to each side of the elevated, indented, dorsal midline. S3–8 laterally carinate, S9–10 lacking carina, S1–S7 with spiniform setae not disposed at one row, S8–S10 with spiniform setae increasing in number posteriorly. Sterna 1–4 lacking spiniform setae, sterna 5–10 with spiniform setae, abundant at sides, scarce at middle. Posterior margin of sterna 1–9 with delicate, minute setae, S10 with a row of stout spiniform setae in posterior margin. Male gonapophyses (Figure 3a) long, surpassing well beyond the posterior margin of sternite 9, divergent in ventral view, sharply pointed, ventral border with a row of eight spines and a long seta at the base of each spine, increasing in robustness apically. Female gonapophyses (Figure 3b, c) surpassing well beyond the posterior margin of sternite 10, external valve slightly longer than internal valve, their ventral border with a basal row of 19 spines, increasing in size and robustness caudad, a long seta at the base of each spine, distal 0.25 bare; lateral valve sharply pointed, central valve roundly tipped. Caudal lamellae (Figure 4) membranous, densely tracheated, with a slight ambarine tint, without nodus. Epiproct (Figure 4a) subovate, 2.5 times longer than their widest part, basal 0.40 of dorsal margin with 32 spines, basal 0.25 of ventral margin with 12 spines, abruptly tapered into a large, triangular tip. Paraproct (Figure 4b) lanceolate, basal 0.25 of dorsal margin with 14 spines, basal 0.45 of ventral margin with 29 spines, tip similar to that of epiproct but shorter, remainder of margins in both epi- and paraprocts with a scarce, minute, very fine setae. Male cerci wider than long, globose (Figure 3a, d), female cerci conical (Figure 3b, c).

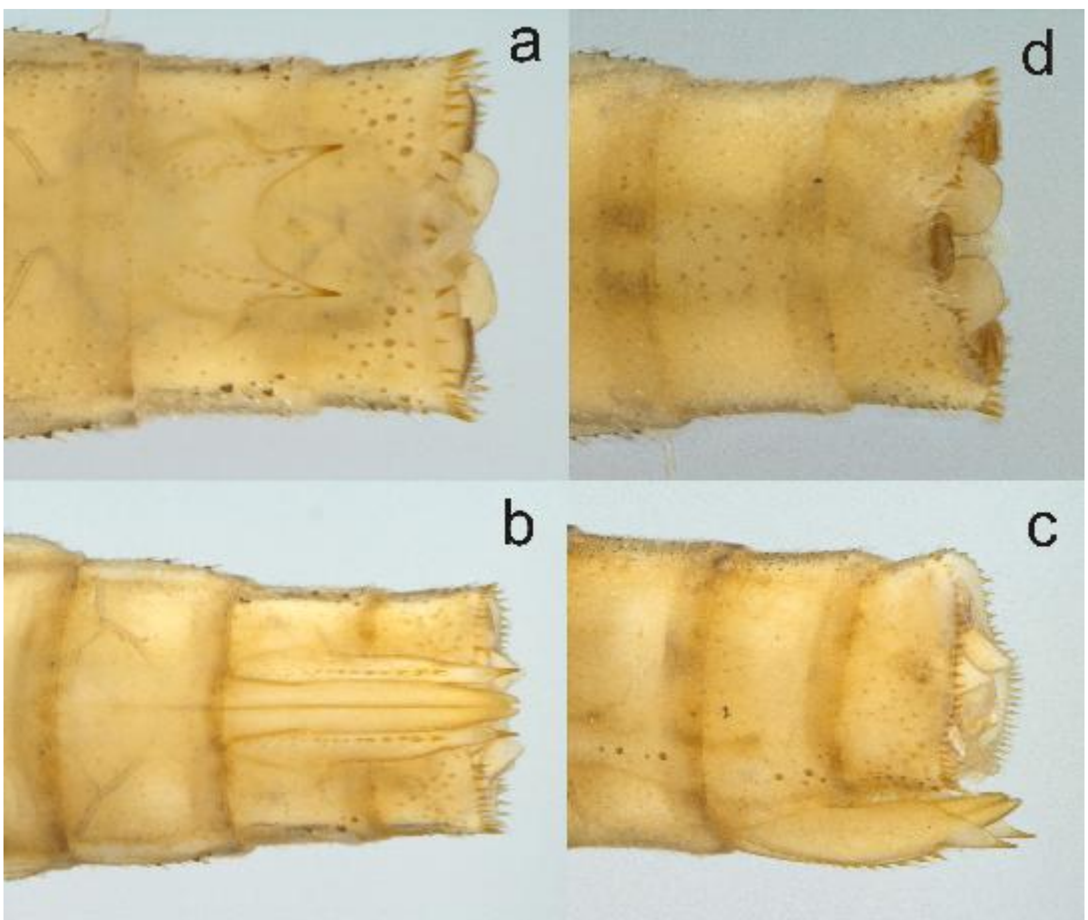

Figure 3. *A. allopterum*, S8 –10 (caudal lamellae detached). (a) Male gonapophyses and cerci, ventral view; (b) female gonapophyses, ventral view; (c) lateral view of female gonapophyses and cerci; (d) male cerci, dorsal view.

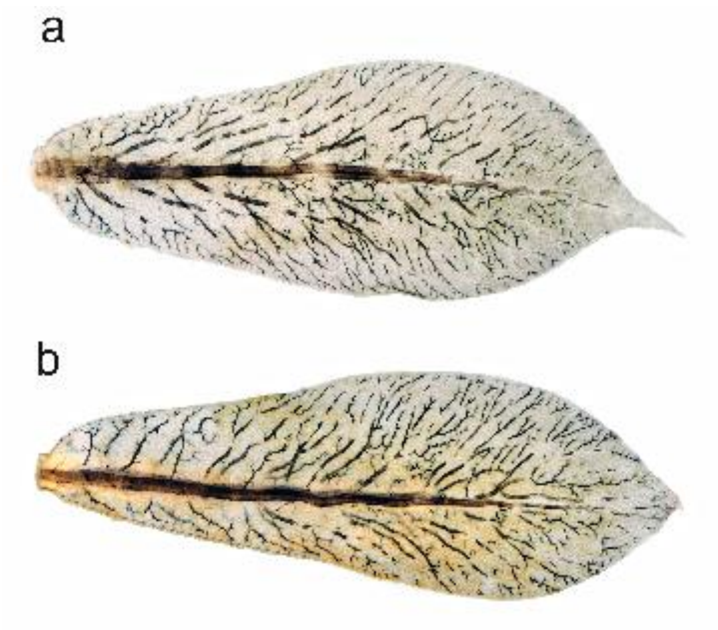

Figure 4. *A. allopterum*, caudal lamellae, left lateral view. (a) Epiproct; (b) paraproct.

Measurements

TL 15.5; AL 6.8–7.0; FfL 1.5; MfL 2.0; HfL 2.5; MWh 3.0; MgL 0.5; FgL 1.10. Ep maximum length 4.7, maximum width 1.8; Pp maximum length 4.9, maximum width 1.8; Ce 0.1.

Diagnosis

Anisagrion allopterum differs from *A. inornatum* (characteristics of the latter in parentheses) by having a larger width of head: 3mm (2.2–2.3); antenna total length 1 .8 (2.0), premental setae 4 +1 (usually 4); lateral margin of prementum usually with seven spiniform setae (1 2 –1 5); paraprocts with 29 spines on ventral series (4 0); frons mostly yellowish (predominantly dark to light brown); tip of ligula narrow (widely convex); distal tarsomeres bicolored (pale).

Habitat

Larvae of *Anisagrion allopterum* were found in artificial lakes associated to aquatic plants of the genus *Myriophyllum* sp. (Haloragaceae) in the Botanical Garden Lankester (Figure

5), and to *Nymphoides* sp. (Menyanthaceae) at the recreational park Doña Ana (Figure 6), both in Paraíso, Cartago Province. During a year of collections, the emergence activity was observed in April in Lankester, and December in lake Doña Ana. Tennessen (2012) reported larvae of *A. inornatum* from a small, shallow stream, with abundant aquatic and semi-aquatic plants, so it is possible that larvae of *A. allopterum* can be found also in pool areas of some streams in Middle America.

Figure 5. *Myriophyllum* sp. (Haloragaceae) in the Botanical Garden Lankester, detail of the larval habitat of *A. allopterum*, Paraíso, Cartago.

Figure 6. Larval habitat in lake Doña Ana, Paraíso, Cartago.

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ARTÍCULO 4

Román-Heracleo, J., M. Springer & R. Novelo-Gutiérrez. (2020). Redescription of the larva of *Neoerythromma cultellatum* (Hagen *in* Selys, 1876) (Odonata: Coenagrionidae: Coenagrioninae). *Zootaxa* 4830(3): 565 – 572.

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Redescription of the larva of *Neoerythromma cultellatum* (Hagen *in* Selys, 1876) (Odonata: Coenagrionidae: Coenagrioninae)

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Abstract

The final instar of *Neoerythromma cultellatum* (Hagen in Selys, 1876) is redescribed and illustrated based upon reared specimens from Turrialba, Cartago, Costa Rica. This is a detailed complement of the original description provided by García-Díaz (1938) and illustrated with high quality photos of the larval morphology. The larva of *N. cultellatum* is characterized by a slender, spinulose, and yellow to yellowish-brown body, premental setae 3+1, five palpal setae, male cerci long, and caudal lamella lanceolate, with obvious node, spotted, and markedly tracheate.

Redescription of the larva of *Neoerythromma cultellatum* (Hagen *in* Selys, 1876) (Odonata: Coenagrionidae: Coenagrioninae)

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Abstract

The final instar of *Neoerythromma cultellatum* (Hagen *in* Selys, 1876) is redescribed and illustrated based upon reared specimens from Turrialba, Cartago, Costa Rica. This is a detailed complement of the original description provided by García-Díaz (1938) and illustrated with high quality photos of the larval morphology. The larva of *N. cultellatum* is characterized by a slender, spinulose, and yellow to yellowish-brown body, premental setae 3+1, five palpal setae, male cerci long, and caudal lamella lanceolate, with obvious node, spotted, and markedly tracheate.

Key words: Costa Rica; Zygoptera; final instar; taxonomy; damselflies.

Resumen

Se redescribe e ilustra el último estadio larval de *Neoerythromma cultellatum* (Hagen *in* Selys, 1876) con base en especímenes criados, provenientes del Cantón de Turrialba, Cartago, Costa Rica. Este es un complemento detallado de la descripción original hecha por García-Díaz (1938), ilustrado con fotos de alta resolución de la morfología larval. La larva de *N. cultellatum* se caracteriza por un cuerpo esbelto, con pequeñas sedas espiniformes y una coloración que va de amarilla a pardo-amarillenta, 3+1 sedas prementales, cinco sedas palpales, cercos del macho alargados, lamelas caudales lanceoladas y con nodo evidente, con manchas y marcadamente traqueadas.

Palabras clave: Costa Rica; Zygoptera; estadio final; taxonomía; libélulas.

Introduction

Neoerythromma Kennedy, 1920 is a small genus within Coenagrionidae, with only two species described so far: the widespread *N. cultellatum* (Hagen *in* Selys, 1876), and *N. gladiolatum* Williamson & Williamson, 1930, endemic to western Mexico (González-Soriano & Novelo-Gutiérrez 1996). This genus is distributed from the southeastern United States through Mexico, to Central America, the Antilles and Venezuela (Garrison *et al.* 2010). Adults of *N. cultellatum* are characterized by their small to medium size (27–31.2mm), with a predominantly blue and black coloration, and with a bright yellow face in males (Garrison *et al.* 2010).

Of the two species, only the larva of *N. cultellatum* is known, but the description provided by García-Díaz (1938) is brief and insufficient to distinguish this species from other coenagrionid larvae. Therefore, the aim of this paper is to provide an updated full description and detailed illustrations of the larva of *N. cultellatum* based upon five exuviae (reared) and six F-0 larvae that complement the description provided by García-Díaz (1938) originally as *Enallagma cultellatum.*

Materials and methods

Mature larvae were collected monthly over one year. The captures were made with an aquatic net and transported to the laboratory for rearing. Emerged adults were maintained alive for a few days and preserved after death in 95% ethanol, together with their exuviae. Additional larvae preserved in ethanol 95%, were also examined. The descriptions and measurements (in mm) were done using a Nikon SMZ 745 stereomicroscope with a calibrated ocular micrometer. Photographs of morphology were taken with a Nikon SMZ25 stereomicroscope and its mounted Nikon DS-U3 camera, and processed with the program NIS elements AR version 4.5. Mandible nomenclature follows Watson (1956) and labium nomenclature follows Corbet (1953). Abbreviations are as follows: AL, abdomen length (without caudal lamella); FfL, fore femur length; HfL, hind femur length; MfL, medium femur length; Ce, cerci; MgL, male gonapophyses length; FgL, female gonapophyses length; MWh, maximum width of head; TL, total length (including caudal lamellae); S1–S10, abdominal segments; F-0, last stadium; Ep, Epiproct; Pp, Paraproct; CATIE (Centro Agronómico Tropical de Investigación y Enseñanza); MZUCR, Museo de Zoología, Universidad de Costa Rica; IEXA, Colección Entomológica "Miguel Angel Morón Ríos" del Instituto de Ecología, A.C. Specimens are deposited in MZUCR and IEXA.

Last stadium larva of *Neoerythromma cultellatum*

(Figures 1–5)

Material examined. Nine F-0 exuviae (5 m##, 4 f#f# reared), seven F-0 larvae (4 m##, 3 f#). COSTA RICA: Turrialba, CATIE (9.8906 N; 83.6545 W; elevation 611 m asl); 11 March 2018 (1 m#, 1 f#, no emergence data); 11 April 2018 (1 m#, 3 f#f#, no emergence data); 24 October 2018 (1 m#, no emergence data); (1 m#, 2 f#f#) larvae, collected 14 June 2018; (2 m##, 1 f#) larvae, collected 24 September 2018. COSTA RICA: San José, San Sebastián, Parque Metropolitano de La Paz. (9.9146N; 84.0728 W; elevation 1137 m asl); 18 August 2018 (2 m#m#, no emergence data); (1 m#) larvae, collected on 22 October

2018. J. Román-Heracleo & Y. Bravo-Méndez legs. Two larvae F-0 (1 m#, 1 f#) deposited at IEXA, all other in MZUCR.

Description

Exuviae and mature larvae mostly yellowish-brown, body slender and spinulose, femora banded, caudal lamellae markedly tracheate (Figure 1).

FIGURE 1. *Neoerythromma cultellatum*, male. Habitus dorsal of the F-0 larva.

Head. Subpentagonal, almost twice as wide as long, wider than thorax and abdomen (Fig. 1). Labrum with anterior margin concave in the middle, with long and short scattered setae on its surface; clypeus mostly glabrous; frons and vertex flat. Occipital margin (Fig. 2a) widely concave; lateral margins of cephalic lobes undulate and converging posteriorly, posterolateral corners angulated, with stout spiniform setae. Antennae (Fig. 2b) 7-segmented, scape and pedicel cylindrical, wider, scape brown to dark-brown, pedicel mostly brown, distal half yellowish, flagellomeres elongated, 3rd antennomere longest, mostly light brown with a pale yellow ring in middle and on distal end, antennomeres 4–6 light brown with apex creamy pale, 7th antennomere translucid, size proportions of antennomeres: 0.65, 0.55, 1.0, 0.75, 0.55, 0.35, 0.25. Compound eyes moderately developed, wider than long, laterally prominent, with black, longitudinal lines. Mandibles (Fig. 2c) with formula: R 1+2345 y a / L 1+2345 0 a b, b=a. Maxilla's galeolacinia (Fig. 2d) with six teeth, three dorsal teeth slightly incurved, of similar length and thickness, with a basal row of seven long thin setae, three ventral teeth of different sizes and thickness, size proportions: apical tooth 1.0, median tooth 0.50, basal tooth a mere spine, with a basal row of thick, stiff setae which increase suddenly in size and thickness apically; maxillary palp gently incurved, ending in a short, stout spine, with long setae on external surface. Ventral pad of hypopharynx subrectangular, anterior margin slightly convex, ventral surface mostly setose, setae large and stiff directed anteriorly, three long setae on each anterolateral corner. Labium: Prementum-postmentum articulation reaching mesocoxae; prementum (Fig. 2e) longer than wide, subrhomboidal, basal half of lateral margins straight and widely divergent apically, on distal half the laterodorsal margin with a row of seven, rarely five, spiniform setae, and a group of three basidorsal spiniform setae; anterior margin of ligula convex, finely serrulated; $3+_1$ premental setae on each side of midline, rarely 3 or $3+_2$. Labial palp (Fig. 2f) with 5 long setae, its apical lobe divided into a squarely truncate dorsal branch, distal margin of which has three small ventral teeth more or less of the same size and thickness, and four dorsal minute denticles, and a ventral branch with a well-developed end hook, slightly decurved; internal margin of palp finely serrate; movable hook scarcely more than half the length of labial palp, sharply pointed.

Thorax. Pronotum (Fig. 2a) yellow to yellowish-brown, subtrapezoidal, mostly bare, posterolateral margin rounded, with 1–2 small, spiniform setae, posterior margin widely convex (Figs 1 and 2a). Pterothorax yellowish-brown, with abundant, minute, spiniform setae with raised brown insertions giving a granulose aspect. Anterior and posterior wing sheaths reaching distal third of S3 (Figure 1). Legs pale cream, slender, long (when fully extended, hind legs reaching posterior margin of S10). Femora and tibiae double-carinated ventrally, with longitudinal rows of spiniform setae on all the surfaces. Femora with one basal and one subapical, narrow, brown band (Figure 1). Tibiae with long, white, regularly spaced setae on external surface, and tridentate setae on distointernal end; pro- and mesotibiae longer than respective femora, metatibiae as long as metafemora. Tarsi with two longitudinal, ventral rows of long, robust setae, and long, delicate setae on dorsal surface; tarsal claws simple, long, strongly curved.

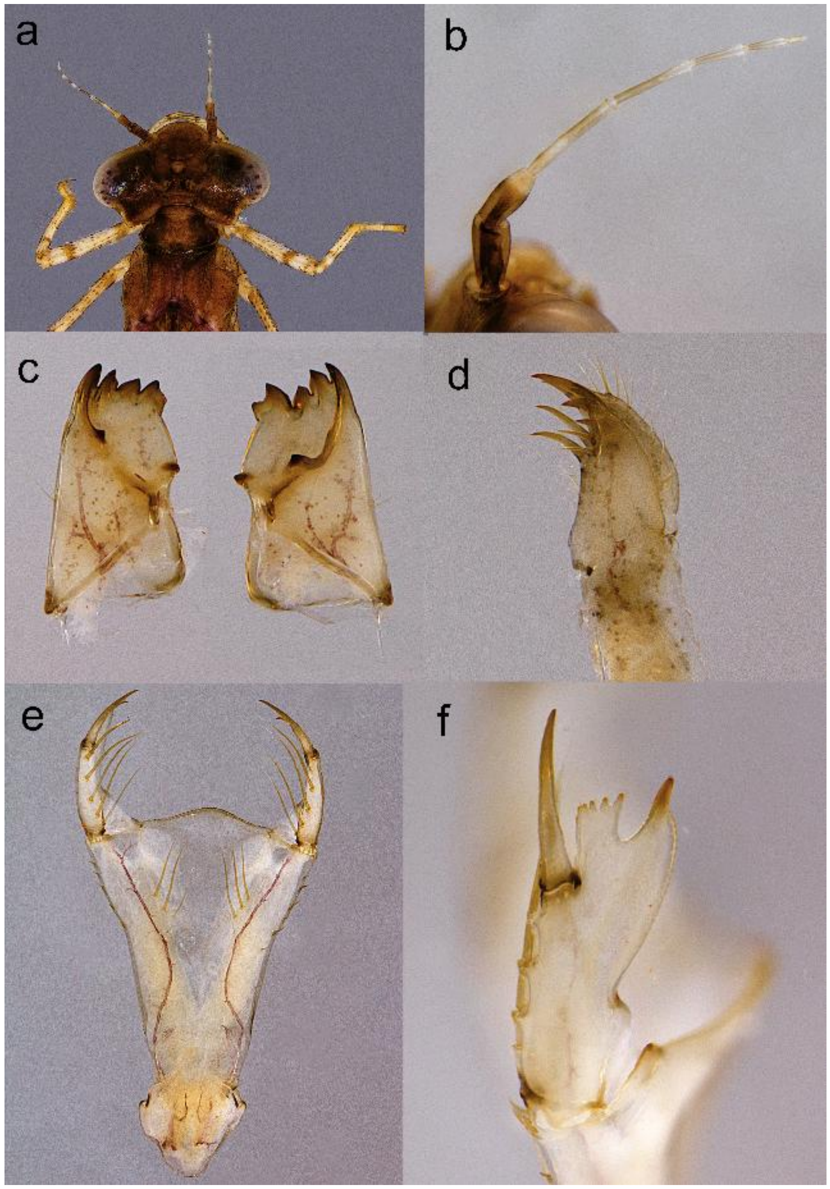

FIGURE 2. *Neoerythromma cultellatum* details of larval morphology. a) Head, dorsal view; b) Right antenna, dorsal view; c) Mandibles, ventrointernal view; d) Right maxilla, dorsal view; e) Prementum, dorsal view; f) Left palp, frontal view.

Abdomen. Cylindrical, yellow to yellowish-brown on dorsum, pale cream colored ventrally, abundantly spinulose (Fig. 1); S3–8 gradually widening posteriorly, then slightly narrowed on S9–10; S3–8 with a dorsal, longitudinal, narrow, dark stripe on each side of midline, ending in a small, dark spot; lateral margins of S1–8 keeled, S2–7 keel beset with small spiniform setae not arranged in one row, ending in 1–2 stouter spiniform setae, S8 keel with small spiniform setae forming one row, ending in one stouter spiniform seta (Fig. 3d–f); lateral margins of S9 lacking keel but ending in a stout spiniform seta; posterior margins of S1–10 with a row of small spiniform setae. S1–8 with a longitudinal, narrow midventral dark stripe. Male gonapophyses (Fig. 3c): Pyramidal, sharply-pointed, tips divergent and slightly surpassing posterior margin of S9, ventral surface with 3–7 spiniform setae which increase in size and thickness caudad (Fig. 3c). Female gonapophyses (Fig. 3e, f): Lateral valvae sharply pointed, nearly reaching posterior margin of S10, with a ventral row of 7–8 spiniform setae which increase in size and thickness posteriorly, a group of 4–7 minute spiniform setae on the basal half of the lateral surface; central valvae shorter, smooth, reaching the basal 0.60 of S10. Caudal lamellae (Fig. 4) lanceolate, mostly translucid, slightly sclerotized on basal half, membranous on distal half, 4–4.5 times longer than their maximum width, with a well-defined nodus at half their length, with brown spots regularly spaced along both margins of the principal, longitudinal tracheae, tracheation more or less dense along dorsal and ventral margins. Epiproct with a row of 26–32 spiniform setae on basal half of dorsal margin, which increase in size and thickness posteriorly, remainder smooth, its ventral margin mostly smooth, with 3–4 minute spiniform setae at extreme base only; a longitudinal keel on both sides of basal half beset with a row of 20–22 small spiniform setae (Fig. 4a). Paraproct with a row of 28–32 spiniform setae on basal half of ventral margin, which increase in size and thickness posteriorly, remainder smooth, its dorsal margin mostly smooth, with 3–4 minute spiniform setae at extreme base; a longitudinal, lateral keel on basal half beset with a row of 24–26 small spiniform setae (Fig. 4b). Male and female cerci as in Figures 3a–c and 3d–f, respectively.

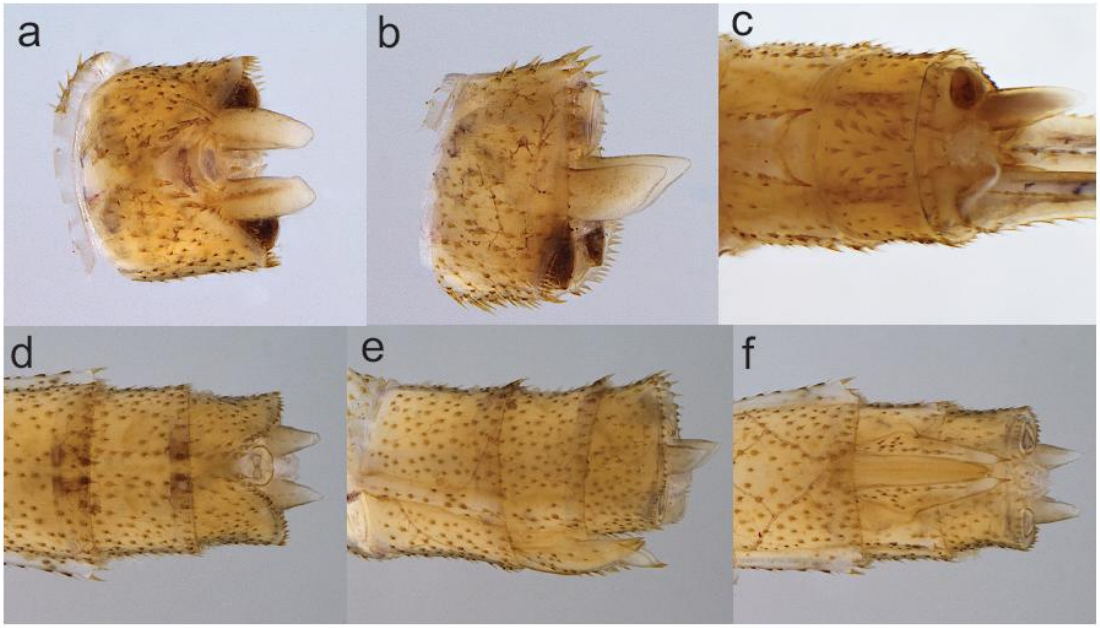

FIGURE 3. *Neoerythromma cultellatum*, S10 (male), S8–10 (female). a) Male cerci, dorsal view; b) Male cerci, lateral view; c) Male gonapophyses, ventral view; d) Female cerci, dorsal view; e) Female cerci and gonapophyses, lateral view; Female cerci and gonapophyses, ventral view.

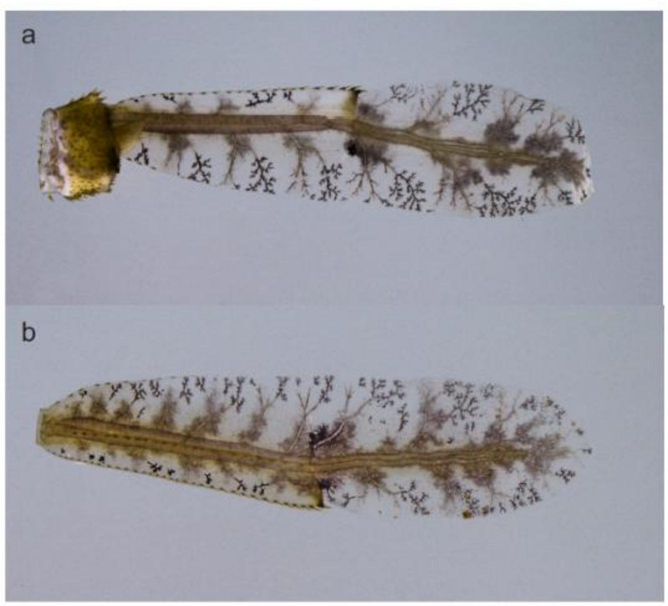

FIGURE 4. *Neoerythromma cultellatum*, caudal lamella, left lateral view. a) Epiproct; b) Paraproct.

Measurements

TL 15.1–17.2; AL 6.5–8.0; MWh 2.8–3.0; FfL 1.2–1.5; MfL 1.8–2.0; HfL 2.4– 3.0; Ce 0.2 (female), 0.4 (male); MgL 0.5; FgL 1.0; EpL 4.8–4.9, maximum width 1.3; PpL 5.0–5.2, max. width 1.1.

Remarks

The description of the larva of *N. cultellatum* provided by García-Díaz (1938) is incomplete, and has only two illustrations. For that reason, we have emphasized in our more detailed description all those structures not treated by him, such as all mouthparts, pronotal disc, wing sheaths, male gonapophyses, and male and female cerci, providing high quality photos for all of them.

Diagnosis

The larva of *N. cultellatum* greatly resembles those of *Enallagma coecum* (Hagen, 1861) and *E. novaehispaniae* Calvert, 1902, from which it can be separated by the following features (in parentheses features of *Enallagma*): premental setae usually 3+1 on each side of midline (one seta); 5 palpal setae (4 palpal setae *E. novaehispaniae*, 3 palpal setae *E. coecum*); male cerci twice as long as wide (one third longer than wide); caudal lamellae with brown spots regularly spaced along both margins of the principal tracheae (caudal lamellae with a continuous, longitudinal, dark stripe constricted at regular intervals).

Habitat

Larvae of *Neoerythromma cultellatum* were found in artificial lagoons located in rural (CATIE) and urban areas (La Paz) (Fig. 5a–b). The two habitats differ from each other, since CATIE has a natural margin and a great abundance and diversity of aquatic plants, and dominated by water lilies, while La Paz lacks aquatic plants and has a concrete margin.

FIGURE 5. Habitat of *Neoerythromma cultellatum*. a) Turrialba, CATIE pond, Costa Rica; b) San José, La Paz, Costa Rica.

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