

Odonata of Costa Rica: Diversity and checklist of species

Alonso Ramírez¹, Dennis R. Paulson² and Carlos Esquivel³

1 Institute of Ecology, University of Georgia, Athens, GA 30602, USA, fax: (706) 542-3344, e-mail: aramirez@arches.uga.edu.

2 Slater Museum of Natural History, University of Puget Sound, Tacoma, WA 98416 USA.

3 Escuela de Ciencias Biológicas, Universidad Nacional, Heredia, Costa Rica.

Received 15-IV-1999. Corrected 28-X-1999. Accepted 10-XI-1999.

Abstract: An updated list of the Odonata of Costa Rica is presented containing 268 species. Since the last published list for the country, 41 additional species have been reported. The country is the best studied in Central America. The most species-rich families are Libellulidae, Coenagrionidae, Gomphidae, and Aeshnidae, together comprising ~75% of the total fauna. Most species in the country are also found in South America, indicating a tendency for wide ranges rather than endemism. However, about a fifth of the species appear to be endemic to the Costa Rica-Panama region. Estimates of the range of the proportion of total world species occurring in Costa Rica lead to predictions of a range of 5 600-9 000 species of Odonata worldwide.

Key words: Odonata, Costa Rica, checklist, aquatic entomology, diversity, tropics.

Members of the order Odonata are among the most familiar groups of insects, perhaps surpassed only by the butterflies (order Lepidoptera). These insects are commonly known as dragonflies and damselflies in English and libélulas or caballitos del diablo in Spanish. Although adults are colorful and easy to spot, especially the males, our knowledge of tropical Odonata is not much greater than that of most other insect groups in tropical regions. Studies on Neotropical Odonata are virtually restricted to taxonomic works, with very few complete faunal lists. Very little is known about the ecology and behavior of most species in this order of aquatic insects.

Studies on Costa Rican Odonata started as early as 1890 with the publication of P. P. Calvert's Odonata chapter in the *Biologia Centrali-Americana* (Calvert 1892-1908). In

that account, 293 species of Odonata were reported as occurring in Mexico and Central America, of which 101 were listed for Costa Rica. In the same work, Calvert estimated 163 species for Costa Rica, based on taxa recorded from adjacent countries but not from Costa Rica at that point. The most recent list of species of Costa Rican Odonata was provided by Paulson (1982), who also presented a list of synonyms that is useful when using old taxonomic works on Odonata.

The objective of this study is to contribute to the knowledge of the Costa Rican fauna by providing an updated checklist of species occurring in the country. In addition, we highlight major characteristics of the Odonata fauna of Costa Rica in contrast with that of other countries in America.

MATERIALS AND METHODS

Data were obtained from the collections and databases of the authors and the Museo de Insectos at the Universidad de Costa Rica. In addition, information was obtained from collections made by S. Brooks, British Museum of Natural History, England (Brooks 1989); T. Donnelly, Binghamton, New York; S. Dunkle, Plano, Texas; G. Harp, State University, Arkansas; and R. Novelo-Gutiérrez, Instituto de Ecología A.C., Mexico.

RESULTS

At present, 268 species of Odonata have been recorded from Costa Rica, distributed among 14 families and 73 genera (Table 1). Four families stand out as the most diverse, in number of both genera and species: Libellulidae, Coenagrionidae, Gomphidae, and Aeshnidae (Fig. 1). The four families combined comprise ~75% of the total Odonata fauna of Costa Rica.

TABLE 1

List of species of the order Odonata from Costa Rica.

Suborder Zygoptera**Polythoridae**

Cora chirripa Calvert, 1907
C. marina Selys, 1868
C. notoxantha Ris, 1918
C. obscura Ris, 1918
C. semiopaca Selys, 1878
C. skinneri Calvert, 1907
Miocora peraltica Calvert, 1917

Calopterygidae

Hetaerina caja (Drury, 1773)
H. capitalis Selys, 1873
H. cruentata (Rambur, 1842)
H. fuscoguttata Selys, 1878
H. majuscula Selys, 1853
H. miniata Selys, 1879
H. occisa Hagen in Selys, 1853
H. sempronina Hagen in Selys, 1853
H. titia (Drury, 1773)

Lestidae

Archilestes grandis (Rambur, 1842)
A. latialatus Donnelly, 1981
A. neblina Garrison, 1982 a
Lestes alacer Hagen, 1861
L. forficula Rambur, 1842
L. henshawi Calvert, 1907
L. sigma Calvert, 1901
L. tenuatus Rambur, 1842
L. tikalus Kormondy, 1959

Perilestidae

Perissolestes magdalenae (Williamson and Williamson, 1924) c
P. remotus (Williamson and Williamson, 1924)

Megapodagrionidae

Heteragrion albifrons Ris, 1918
H. atrolineatum Donnelly, 1992 b

H. erythrogastrum Selys, 1886
H. majus Selys, 1886
H. mitratum Williamson, 1919 c
Philogenia carrillica Calvert, 1907
P. championi Calvert, 1901
P. expansa Calvert, 1924
P. lankesteri Calvert, 1924
P. peacocki Brooks, 1989 a
P. terraba Calvert, 1907
Thaumatoneura inopinata McLachlan, 1897

Pseudostigmatidae

Mecistogaster linearis (Fabricius, 1776)
M. modesta Selys, 1860
M. ornata Rambur, 1842
Megaloprepus caerulatus (Drury, 1782)
Pseudostigma aberrans Selys, 1860
P. accedens Selys, 1860 c

Platystictidae

Palaemnema baltodanoi Brooks, 1989 a
P. chiriquita Calvert, 1931
P. collaris Donnelly, 1992 b
P. dentata Donnelly, 1992 b
P. distadens Calvert, 1931
P. gigantula Calvert, 1931
P. melanota Ris, 1918
P. nathalia Selys, 1886
P. paulirica Calvert, 1931
P. reventazoni Calvert, 1931

Protoneuridae

Neoneura amelia Calvert, 1903
N. esthera Williamson, 1917
Protoneura amatoria Calvert, 1907
P. aurantiaca Selys, 1886
P. sulfurata Donnelly, 1989 a
Psaironeura remissa (Calvert, 1903)
P. selvatica Esquivel, 1993 a

Continues...

Table 1 (continued)

Coenagrionidae

Acanthagrion inexpectum Leonard, 1977
A. speculum Garrison, 1985 ad
A. trilobatum Leonard, 1977
Anisagrion allopterum Selys, 1876
A. kennedyi Leonard, 1937
Argia adamsi Calvert, 1902
A. anceps Garrison, 1996 ad
A. chelata Calvert, 1902
A. cupraurea Calvert, 1902
A. cuprea (Hagen, 1861) c
A. difficilis Selys, 1865
A. elliptica Selys, 1865 c
A. extranea (Hagen, 1861)
A. fissa Selys, 1865
A. frequentula Calvert, 1907
A. gaumeri Calvert, 1907 c
A. indicatrix Calvert, 1902
A. insipida Hagen in Selys, 1865
A. johannella Calvert, 1907
A. medullaris Hagen in Selys, 1865
A. oculata Hagen in Selys, 1865
A. oenea Hagen in Selys, 1865
A. pocohana Calvert, 1907
A. popoluca Calvert, 1902
A. pulla Hagen in Selys, 1865
A. rogersi Calvert, 1902
A. talamanca Calvert, 1907
A. terira Calvert, 1907
A. tezpi Calvert, 1902
A. translata Hagen in Selys, 1865
A. ulmeca Calvert, 1902
A. underwoodi Calvert, 1907
A. variabilis Selys, 1865
Chrysobasis lucifer Donnelly, 1967
Enallagma civile (Hagen, 1861)
E. novaehispaniae Calvert, 1907
Ischnura capreolus Hagen, 1861
I. hastata (Say, 1839)
I. ramburii (Selys, 1850)
Leptobasis vacillans Hagen in Selys, 1877
Metaleptobasis bovilla Calvert, 1907
M. westfalli Cumming, 1954
Nehalennia minuta (Selys, 1857)
Neoerythromma cultellatum (Selys, 1876)
Telebasis aurea May, 1992 a
T. corallina (Selys, 1876)
T. digiticollis Calvert, 1902
T. filiola (Perty, 1834)
T. garleppi Ris, 1918
T. griffinii (Martin, 1896)
T. isthmica Calvert, 1902
T. salva (Hagen, 1861)

Suborder Anisoptera**Aeshnidae**

Aeshna cornigera Brauer, 1865
A. jalapensis Williamson, 1908

A. psilus Calvert, 1947
A. williamsoniana Calvert, 1905 c
Anax amazili (Burmeister, 1839)
A. concolor Brauer, 1865
Coryphaeschna adnexa (Hagen, 1861)
C. amazonica De Marmels, 1989 bd
C. apeora Paulson, 1994 a
C. diapyra Paulson, 1994 a
C. viriditas Calvert, 1952
Gynacantha auricularis Martin, 1909 c
G. caudata Karsch, 1891
G. gracilis (Burmeister, 1839)
G. laticeps Williamson, 1923
G. membranalis Karsch, 1891
G. mexicana Selys, 1868
G. nervosa Rambur, 1842
G. tibiata Karsch, 1891
Neuraeschna maya Belle, 1989 b
Remartinia luteipennis (Burmeister, 1839)
Staurophlebia reticulata (Burmeister, 1839)
Triacanthagyna caribbea Williamson, 1923
T. ditzleri Williamson, 1923
T. satyrus (Martin, 1909)
T. septima (Selys, 1857)

Gomphidae

Agriogomphus tumens (Calvert, 1905)
Aphylla obscura (Kirby, 1899)
A. protracta (Hagen in Selys, 1859) d
Archaeogomphus furcatus Williamson, 1923
Desmogomphus paucinervis (Selys, 1873)
Epigomphus armatus Ris, 1918
E. camelus Calvert, 1905
E. corniculatus Belle, 1989 a
E. echeverrii Brooks, 1989 a
E. houghtoni Brooks, 1989 a
E. quadracies Calvert, 1903
E. subobtusus Selys, 1878
E. subsimilis Calvert, 1920
E. tumefactus Calvert, 1903
E. verticicornis Calvert, 1908
Erpetogomphus bothrops Garrison, 1994 bd
E. constrictor Ris, 1918 c
E. elaphe Garrison, 1994 bd
E. eutainia Calvert, 1905 c
E. schausi Calvert, 1919 c
E. tristani Calvert, 1912
Perigomphus pallidistylus (Belle, 1972)
Phyllocycla volsella (Calvert, 1905)
Phyllogomphoides appendiculatus (Kirby, 1899)
P. bifasciatus (Hagen in Selys, 1878)
P. burgosi Brooks, 1989 a
P. pugnifer Donnelly, 1979
P. suasus (Selys, 1859)
Progomphus anomalus Belle, 1973 c
P. clendonii Calvert, 1905
P. longistigma Ris, 1918
P. mexicanus Belle, 1973

Continues..

Table 1 (continued)

P. pygmaeus Selys, 1873

Cordulegastridae
Cordulegaster godmani McLachlan, 1878

Corduliidae
Neocordulia batesi (Selys, 1871)
N. campana May and Knopf, 1988 b
N. griphus May, 1991 a

Libellulidae
Anatya normalis Calvert, 1899
Brachymesia furcata (Hagen, 1861)
B. herbida (Gundlach, 1889)
Brechmorhoga nubecula (Rambur, 1842)
B. pertinax (Hagen, 1861)
B. praecox (Hagen, 1861)
B. rapax Calvert, 1898
B. vivax Calvert, 1906
Cannaphila insularis Kirby, 1889
C. mortoni Donnelly, 1992 b
C. vibex (Hagen, 1861)
Dythemis multipunctata Kirby, 1894
D. sterilis Hagen, 1861
Elasmothemis cannacrioides (Calvert, 1906)
Erythemis attala (Selys, 1857)
E. haematogastra (Burmeister, 1839)
E. mithroides (Brauer, 1900)
E. peruviana (Rambur, 1842)
E. plebeja (Burmeister, 1839)
E. simplicicollis (Say, 1839)
E. vesiculosa (Fabricius, 1775)
Erythrodiplax abjecta (Rambur, 1842)
E. andagoya Borror, 1942
E. berenice (Drury, 1770) c
E. castanea (Burmeister, 1839)
E. famula (Erichson, 1848)
E. fervida (Erichson, 1848)
E. funerea (Hagen, 1861)
E. fusca (Rambur, 1842)
E. kimminsi Borror, 1942
E. umbrata (Linnaeus, 1758)
Idiataphe amazonica (Kirby, 1889) c
I. cubensis (Scudder, 1866)
Libellula croceipennis Selys, 1868
L. foliata (Kirby, 1889)
L. herculea Karsch, 1889
L. mariae Garrison, 1992 a
Macrothemis aurimaculata Donnelly, 1984 b
M. delia Ris, 1913
M. extensa Ris, 1913
M. hemichlora (Burmeister, 1839)
M. imitans Karsch, 1890
M. inacuta Calvert, 1898
M. inequiunguis Calvert, 1895
M. musiva Calvert, 1898
M. pseudimitans Calvert, 1898
Miathyria marcella (Selys, 1857)
M. simplex (Rambur, 1842)
Micrathyria aequalis (Hagen, 1861)
M. atra (Martin, 1897)
M. catenata Calvert, 1909
M. dictynna Ris, 1919
M. didyma (Selys, 1857)
M. hagenii Kirby, 1890
M. laevigata Calvert, 1909
M. mengeri Ris, 1919
M. ocellata Martin, 1897
M. pseudeximia Westfall, 1992 bd
M. schumanni Calvert, 1906
M. tibialis Kirby, 1897 c
Nephepeltia chalconota Ris, 1919 c
N. phryne (Perty, 1834)
Oligoclada umbricola Borror, 1931 c
Orthemis biolleyi Calvert, 1906
O. cultriformis Calvert, 1899
O. discolor (Burmeister, 1839) c
O. ferruginea (Fabricius, 1775)
O. levis Calvert, 1906
Paltothemis lineatipes Karsch, 1890
Pantala flavescens (Fabricius, 1798)
P. hymenaea (Say, 1839)
Perithemis domitia (Drury, 1773)
P. electra Ris, 1930
P. mooma Kirby, 1889
Pseudoleon superbus (Hagen, 1861)
Rhodopygia hinei Calvert, 1907
Sympetrum illotum (Hagen, 1861)
S. nigrocreatum Calvert, 1920
Tauriphila argo (Hagen, 1869)
T. australis (Hagen, 1867)
T. azteca Calvert, 1906
Tholymis citrina Hagen, 1867
Tramea abdominalis (Rambur, 1842)
T. binotata (Rambur, 1842)
T. calverti Muttikowski, 1910
T. insularis Hagen, 1861 c
T. onusta Hagen, 1861
Uracis fastigiata (Burmeister, 1839)
U. imbuta (Burmeister, 1839)
U. turrialba Ris, 1919

Key to changes from Paulson (1982): a- newly described from Costa Rica, b- newly described from elsewhere, originally or subsequently recorded from Costa Rica, c- newly recorded from Costa Rica, d- reidentified, previously listed under a different name.

TABLE 2

Name changes from the list of Paulson (1982).

Paulson 1982	Current name	Reason	Source
<i>Anomalagrion hastatum</i>	<i>Ischnura hastata</i>	New synonymy	De Marmels 1987
<i>Aphylla ambigua</i>	<i>A. protracta</i>	New synonymy	Garrison 1986
<i>Argiallagma minutum</i>	<i>Nehalennia minuta</i>	New synonymy	De Marmels 1984
<i>Coryphaeschna luteipennis</i>	<i>Remartinia luteipennis</i>	Genericsplit	Carvalho 1992
<i>Coryphaeschna perrensi</i>	<i>C. amazonica</i>	New sp. Described	Paulson 1994
<i>Dythemis cannaerioides</i>	<i>Elasmothemis cannaerioides</i>	Genericsplit	Westfall 1988
<i>Erpetogomphus elaps</i>	<i>E. elaphe</i>	New sp. Described	Garrison 1994
<i>Erpetogomphus viperinus</i>	<i>E. bothrops</i>	New sp. Described	Garrison 1994
<i>Hetaerina macropus</i>	<i>H. occisa</i>	New synonymy	Garrison 1990
<i>Hetaerina maxima</i>	<i>H. capitalis</i>	New synonymy	Garrison 1990
<i>Lepthemis attala</i>	<i>Erythemis attala</i>	New synonymy	Bridges 1993
<i>Lepthemis haematogastra</i>	<i>Erythemis haematogastra</i>	New synonymy	Bridges 1993
<i>Lepthemis mithroides</i>	<i>Erythemis mithroides</i>	New synonymy	Bridges 1993
<i>Lepthemis peruviana</i>	<i>Erythemis peruviana</i>	New synonymy	Bridges 1993
<i>Lepthemis plebeja</i>	<i>Erythemis plebeja</i>	New synonymy	Bridges 1993
<i>Lepthemis simplicicollis</i>	<i>Erythemis simplicicollis</i>	New synonymy	Bridges 1993
<i>Lepthemis vesiculosa</i>	<i>Erythemis vesiculosa</i>	New synonymy	Bridges 1993
<i>Macrothemis tessellata</i>	<i>M. inequinguis</i>	Subspecies removed from species	Garrison 1991
<i>Micrathyria eximia</i>	<i>M. pseudeximia</i>	New sp. Described	Westfall 1992
<i>Neocordulia longipollex</i>	<i>N. batesi longipollex</i>	Combined with another species	May 1991

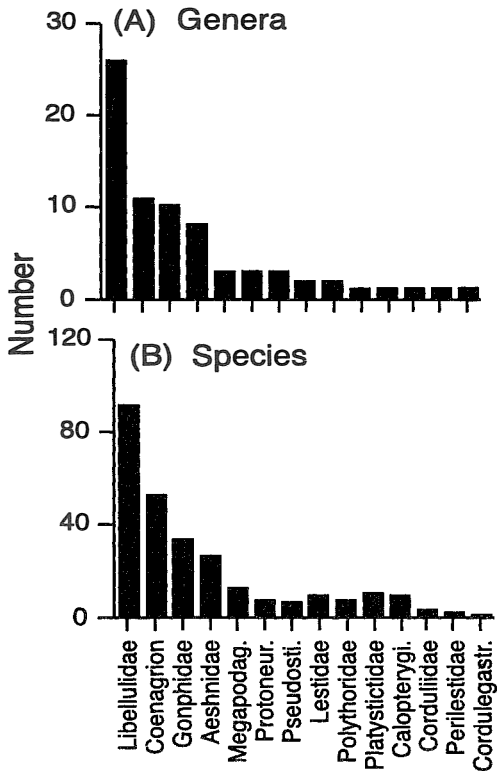


Fig. 1. Distribution of genera (A) and species (B) among families of the order Odonata in Costa Rica.

Paulson (1982) listed 227 species of Odonata from Costa Rica. The present list contains 268 species, 41 more than Paulson recorded. The difference in the number of species is the result of the naming of previously undescribed species (25, of which 5 had been recorded under another name) and the recording of additional species (21) from the country. Three species were recorded as questionable in Paulson's list: *Hetaerina infecta* (old record not confirmed), *Acanthagrion quadratum* (misidentified, actually *A. speculum*), and *Anax junius* (old record not confirmed). Only one species has been deleted from the list, *Perithemis thais* (now considered an undescribed species). Finally, the names of 20 of the species on Paulson's (1982) list have changed (Table 2) because of synonymies or misidentifications.

The proportion of undescribed to described species in a region should decrease as the region becomes better known. Paulson (1982) listed 23 undescribed species that occurred in Costa Rica, representing 1.0% of the known fauna. Subsequently, 11 of these species have been described, one as a subspecies, and 13

species not known to Paulson have been described as well. At present, there are still at least 11 Costa Rican species awaiting description (*i.e.*, one *Miocora*, four *Palaemnema*, two *Argia*, one *Leptobasis*, one *Gynacantha*, one *Micrathyria*, and one *Perithemis*), representing 0.4% of the known fauna.

The broad distributional patterns of the Costa Rican fauna were analyzed (Table 3). A surprisingly large proportion (about one-fifth) appear to be endemic either to Costa Rica (13.1%) or the Costa Rica-Panama region (6.7%). Another one-fourth (25.7%) of the species are endemic to Middle America region (Mexico to Panama). Almost half of the species clearly have South American affinities, either reaching their northern limit in Costa Rica (5.6%) or widespread in Middle and South America (40.2%), although their area of origin is only speculative. Only a small proportion of the fauna clearly comes from the north, reaching its southern limit in Costa Rica/Panama (6.3%), or is widespread in North, Middle, and South America (4.5%). A single species, *Tramea insularis*, is largely restricted to the West Indies and may be only a vagrant in Costa Rica.

TABLE 3

*Origin of the Costa Rican Odonata fauna
(in percentage, total 268 species).*

	Species	Percentage (%)
Middle and South America	103	38.4
Primarily Middle America	69	25.7
Costa Rica only	35	13.1
Costa Rica-Panama only	18	6.7
Primarily South America	17	6.3
North and Middle America	13	4.9
Widespread	12	4.5
West Indies	1	0.4

DISCUSSION

The list of species presented here represents a significant advance in comparison with previous accounts; however, our list is by no means a final one. Some regions of the country remain poorly explored, for example the southern parts of both the Cordillera de Talamanca and the

Caribbean lowlands. Several families remain poorly collected, especially those that inhabit small forested streams. In addition, several genera (*e.g.*, *Argia*) need to be reviewed to clarify the number of species they include. The number of Odonata species that occur in Costa Rica is not easy to predict, but we suggest that the present list includes at least 80% of the fauna, giving a potential total of ~340 species.

With 268 species known to occur, the Odonata fauna of Costa Rica is surely the best known of all Central American countries. Panama and Guatemala, with over 200 species each (D. Paulson unpublished information), are even less well explored than Costa Rica. Other well-studied Neotropical countries that support richer faunas are much larger than Costa Rica. For example, Brazil has over 650 species (D. Paulson unpublished information), Venezuela 455 (De Marmels 1990), and Mexico 330 (González-Soriano and Novelo-Gutiérrez 1996), but Costa Rica is only about 0.7%, 7%, and 3% of the size of those three countries, respectively, and has a more limited range of environments. Thus Costa Rica has a rich dragonfly fauna for its size.

Analysis of general distribution patterns of the Odonata species recorded in Costa Rica confirms the tropical origin of its fauna. Most species have wide distributions in Middle and South America (Table 3). Although 13.1% of the fauna is endemic to Costa Rica, this is likely the result of poor sampling efforts in adjacent countries rather than such a high degree of endemism. Studies of other taxa indicate that most tropical insects are widely distributed and that high levels of endemism or patchy distributions are probably a sampling artifact (*e.g.*, Richards 1978, Janzen 1986, Gaston *et al.* 1996).

The most recent estimation of the total number of Odonata species was of 5 600 (Bridges 1994). However, many more species remain to be discovered in poorly collected regions, such as most of Central America. Following the procedure used by Gaston *et al.* (1996) for Hymenoptera, we use the present list to speculate about the total number of species of Odonata worldwide. The lower

limit of such an estimate will be the 5 600 known species, of which Costa Rica has 4.8%. However, studies of other animal and plant groups indicated that Costa Rica has from 3-10% of the global species richness of most groups (Gaston *et al.* 1996). In that context, if we assume that Costa Rica has between 3% and 4.8% of the total Odonata fauna, then the potential total number of species in the order is in the range of 5 600 - 9 000. Our estimate is in general agreement with a previous one that suggested the world Odonata fauna to be composed of <10 000 species (Tennessen 1997).

In conclusion, the order Odonata in Costa Rica, although better studied than in other Central American countries, still needs a lot of attention. The distribution of most species is imperfectly known, and nothing is known about the ecology and behavior of virtually all species. More significantly at this time of rapidly vanishing natural habitats, we have no estimate of what percent of the species are protected within the boundaries of national parks and other protected areas. The larvae could be important indicators in monitoring water quality in rivers and lakes, but only half of the species in the country have their larval morphology described (Ramírez 1997), and only the general habitat of most of them is known.

RESUMEN

Se presenta una lista actualizada de los Odonata de Costa Rica, la cual contiene 268 especies. A pesar de ello, se espera que algunas especies más se agregen en el futuro. En comparación con trabajos anteriores, el número de especies para Costa Rica se incrementó en 41, siendo el país mejor estudiado de Centro América. Las familias con mayor diversidad de especies son: Libellulidae, Coenagrionidae, Gomphidae, y Aeshnidae, que en conjunto representan ~75% del total de la fauna de Odonata en Costa Rica. La mayoría de las especies del país también se encuentran en Sur América, lo que indica una inclinación hacia ámbitos de distribución amplios, mas que altos grados de endemismo. Sin embargo, el 18% de las especies es aparentemente endémico de Costa Rica y Panamá. Con base en los números aquí presentados, se esperaría que la fauna mundial de Odonata se encuentre dentro del ámbito de 5 600 a 9 000 especies.

ACKNOWLEDGMENTS

We are grateful to the Museo de Insectos at Universidad de Costa Rica, S. Brooks, T. Donnelly, S. Dunkle, G. Harp, and R. Novelo-Gutiérrez for sharing their data on Costa Rican Odonata. A. Ramírez was supported by the National Science Foundation (grant DEB-95-28434) during the writing of this paper.

REFERENCES

- Bridges, C.A. 1993. Catalogue of the family-group, genus-group and species-group names of the Odonata of the World. Champaign, IL, privately published.
- Brooks, S.J. 1989. Odonata collected from Guanacaste National Park, Costa Rica, July 1988. *Not. Odonatol.* 3: 49-52.
- Calvert, P. P. 1892-1908. Odonata. p. 17-420. *In* F.D. Godwin. (ed.). *Biologia Centrali-Americana*. Porter and Dulau, London.
- Carvalho, A.L. 1992. Revalidation of the genus *Remartinia* Navás, 1911, with the description of a new species and a key to the genera of Neotropical Aeshnidae (Anisoptera). *Odonatologica* 21: 289-298.
- De Marmels, J. 1984. The genus *Nehalennia* Selys, its species and their phylogenetic relationships (Zygoptera: Coenagrionidae). *Odonatologica* 13: 501-527.
- De Marmels, J. 1987. *Ischnura (Anomalagrion) cruzi* sp. n., eine neue Kleinlibelle aus Kolumbien (Odonata: Coenagrionidae). *Mitteil. Ent. Gesell. Basel N.F.* 37: 1-6.
- De Marmels, J. 1990. An updated checklist of Odonata of Venezuela. *Odonatologica* 19: 333-345.
- Garrison, R.W. 1986. The genus *Aphylla* in Mexico and Central America, with a description of a new species, *Aphylla angustifolia* (Odonata: Gomphidae). *Ann. Ent. Soc. Am.* 79: 938-944.
- Garrison, R.W. 1990. A synopsis of the genus *Hetaerina* with descriptions of four new species (Odonata: Calopterygidae). *Trans. Am. Ent. Soc.* 116: 175-259.
- Garrison, R.W. 1991. A synonymic list of the New World Odonata. *Argia* 3: 1-30.

- Garrison, R.W. 1994. A revision of the New World genus *Erpetogomphus* Hagen in Selys (Odonata: Gomphidae). *Tijd. v. Ent.* 137: 173-269.
- Gaston, K.J., I.D. Gauld & P. Hanson. 1996. The size and composition of the hymenopteran fauna of Costa Rica. *J. Biogeogr.* 23: 105-113.
- González-Soriano, E. & R. Novelo-Gutiérrez. 1996. Odonata. p. 147-167. In J. Llorente-Bousquets, A.N. García-Aldrete & E. González-Soriano. (eds.). Biodiversidad, taxonomía, y biogeografía de artrópodos de México: Hacia una síntesis de su conocimiento. Universidad Nacional Autónoma de México, Mexico, D.F.
- Janzen, D.H. 1986. Biogeography of an unexceptional place: what determines the saturniid and sphingid moth faunas of Santa Rosa National Park, Costa Rica, and what does it mean to conservation biology? *Brenesia* 25/26: 51-87.
- May, M.L. 1991. A review of the genus *Neocordulia*, with a description of *Mesocordulia* subgen. nov. and of *Neocordulia griphus* spec. nov. from Central America, and a note on *Lauromacromia* (Odonata: Corduliidae). *Folia Entomol. Mex.* 82: 17-67.
- Paulson, D.R. 1982. Odonata. p. 249-277. In S.H. Hurlbert & A. Villalobos- Figueroa. (eds.). Aquatic Biota of Mexico, Central America, and the West Indies. San Diego State University, San Diego, California.
- Paulson, D.R. 1994. Two new species of *Coryphaeschna* from Middle America, and a discussion of the red species of the genus. *Odonatologica* 23: 379-398.
- Ramírez, A. 1997. Lista de las especies de Odonata de Costa Rica que cuentan con su náyade descrita. *Rev. Biol. Trop.* 44/45: 225-232.
- Richards, O.W. 1978. The social wasps of the Americas excluding the Vespinae. British Museum (Natural History), London.
- Tennessen, K.J. 1997. The rate of species descriptions in Odonata. *Ent. News* 108: 122-126.
- Westfall, M.J. 1988. *Elasmothemis* gen. nov., a new genus related to *Dythemis* (Anisoptera: Libellulidae). *Odonatologica* 17: 419-428.
- Westfall, M.J. 1992. Notes on *Micrathyria*, with descriptions of *M. pseudeximia* sp. n., *M. occipita* sp. n., *M. dunklei* sp. n. and *M. divergens* sp. n. (Anisoptera: Libellulidae). *Odonatologica* 21: 203-218.