

BULLETIN OF AMERICAN ODONATOLOGY

connata

San Alfonso,
Santiago
CHILE



basifusca

San Enrique,
Baja California Sur,
Mexico



Volume 6 Number 4

COMMENTS ON THE *ERYTHRODIPLAX CONNATA* (BURMEISTER, 1839)
GROUP, WITH THE ELEVATION OF *E. FUSCA* (RAMBUR, 1842), *E.*
MINUSCULA (RAMBUR, 1842), AND *E. BASIFUSCA* (CALVERT, 1895) TO
FULL SPECIES (ANISOPTERA: LIBELLULIDAE)

10 January 2003

Dennis Paulson, p. 101-110

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WITH THE ELEVATION OF *E. FUSCA* (RAMBUR, 1842), *E. MINUSCULA* (RAMBUR,
1842), AND *E. BASIFUSCA* (CALVERT, 1895) TO FULL SPECIES (ANISOPTERA:
LIBELLULIDAE)

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ABSTRACT

The *Erythrodiplax connata* group is revised, based on examination of 855 specimens. *E. connata* of Borror (1942) is divided into four species: *E. connata* (Burmeister, 1839), *E. fusca* (Rambur, 1842), *E. minuscula* (Rambur, 1842), and *E. basifusca* (Calvert, 1895). *E. fusca* and *E. minuscula* had been previously considered subspecies of *E. connata*, while *E. basifusca* is resurrected for northern populations of "*E. connata connata*." The remaining species of Borror's *connata* group - *E. abjecta* (Rambur, 1842), *E. atroterminata* Ris, 1911, *E. cauca* Borror, 1942, *E. cleopatra* Ris, 1911, *E. ines* Ris, 1911, *E. justiniana* (Selys, 1857), *E. media* Borror, 1942, *E. melanorubra* Borror, 1942, and *E. paraguayensis* (Förster, 1905) - are considered valid, with the addition of *E. bromeliicola* Westfall, 2000. A population in the Andes of Argentina is similar to *E. fusca* but is possibly specifically distinct. *Diplax portoricana* Kolbe, 1888, is probably a synonym of *E. justiniana* rather than *E. connata*, and *Diplax fraterna* Hagen, 1873, is considered a nomen nudum rather than a synonym of *E. connata*.

INTRODUCTION

The *Erythrodiplax connata* group, based on *E. connata* (Burmeister), comprises a set of species occurring from eastern North America south throughout the Neotropical region, including the West Indies, to southern South America (Table 1). Although Borror (1942) greatly clarified earlier confusion in the taxonomy of this group in his monograph, confusion has persisted in the apparent distribution and species status of three nominal subspecies of *Erythrodiplax connata* (*E. c. connata* [Burmeister], *E. c. fusca* [Rambur], and *E. c. minuscula* [Rambur]) and their closest relatives. Borror (1942: 150) himself admitted "the present taxonomic arrangement, although based on considerable study, is somewhat provisional." He further stated about *E. connata*, "In spite of the considerable variation in size and color of the different forms, they appear to be conspecific, as

the structure of the penis is relatively similar in all of them [italics mine], and the various forms appear to intergrade" (Borror 1942: 159). Borror based many of his taxonomic arrangements on penis structure, but two rather different-looking taxa (*E. famula* [Erichson] and *E. lativittata* Borror) that he considered conspecific because of their identical penes have since been found to be sympatric with no evidence of interbreeding (De Marmels 1989). No change has been made in the taxonomy of the *connata* group since 1942.

I consider some species of the *connata* group sufficiently distinct that I did not include them in this study. *E. atroterminata* Ris has dark wingtips, *E. ines* Ris has very extensive color at the wing base, and *E. paraguayensis* (Förster) is much smaller than the other species. None of these species is likely to be mistaken for the remaining members of the group. I also examined no specimens of the scarcely known *E. cauca* Borror but have assessed it based on Borror's (1942) description.

MATERIALS

Specimens of all three subspecies of *E. connata* were examined, with particular search for evidence of intergradation among any of them. In addition, specimens of most of the other species in the *connata* group were examined, as they are very similar to one another, and understanding them is necessary to understand the distribution and characteristics of those forms that had been lumped with *E. connata* itself. Females are extremely similar in the species of this group, and I base the conclusions drawn below on the study of males, although I looked at females in all populations discussed. Specimens were examined (Appendix 1) from the Florida State Collection of Arthropods, University of Michigan Museum of Zoology, and the collections of T. W. Donnelly, R. W. Garrison, and D. R. Paulson.

THE TWO POPULATIONS OF
ERYTHRODIPLAX CONNATA CONNATA ARE
DISTINCT SPECIES

Named Taxon	Type Locality	Borror 1942	this study
<i>Libellula abjecta</i> Rambur, 1842	Colombia	valid species	same
<i>Diplax ambusta</i> Hagen, 1867	Cardenas, Cuba	syn <i>justiniana</i>	same
<i>Erythrodiplax atroterminata</i> Ris, 1911	Rio Grande do Sul, Brazil	valid species	same
<i>Trithemis basifusca</i> Calvert, 1895	Baja California, Mexico	syn <i>abjecta</i>	valid species
<i>Erythrodiplax bromeliicola</i> Westfall, 2000	Bath, Jamaica	not treated	valid species
<i>Erythrodiplax cauca</i> Borror, 1942	Cauca, Colombia	valid species	same
<i>Libellula chloropleura</i> Brauer, 1865	Chile	syn <i>connata</i>	same
<i>Erythrodiplax cleopatra</i> Ris, 1911	Callao, Peru, and Arica, Chile	valid species	same
<i>Libellula communis</i> Rambur, 1842	Chile	syn <i>connata</i>	same
<i>Libellula connata</i> Burmeister, 1839	Valparaiso, Chile	valid species	same
<i>Diplax fraterna</i> Hagen, 1873	West Indies	syn <i>justiniana</i>	nomen nudum
<i>Libellula fusca</i> Rambur, 1842	Cayenne, French Guiana	subsp <i>connata</i>	valid species
<i>Libellula incompta</i> Rambur, 1842	Cayenne, French Guiana	syn <i>fusca</i>	same
<i>Erythrodiplax ines</i> Ris, 1911	Santa Inez, Ecuador	valid species	same
<i>Libellula justiniana</i> Selys, 1857	Cuba	valid species	same
<i>Libellula leontina</i> Brauer, 1865	Chile	syn <i>connata</i>	same
<i>Erythrodiplax media</i> Borror, 1942	Cachoeira, Brazil	valid species	same
<i>Erythrodiplax melanorubra</i> Borror, 1942	Campamiento, Peru	valid species	same
<i>Libellula minuscula</i> Rambur, 1842	North America	subsp <i>connata</i>	valid species
<i>Diplacodes paraguayensis</i> Förster, 1905	Costa Aquaray, Paraguay	valid species	same
<i>Erythrodiplax ponderosa</i> Karsch, 1891	Ecuador	syn <i>abjecta</i>	same
<i>Diplax portoricana</i> Kolbe, 1888	Puerto Rico	syn <i>connata</i>	syn <i>justiniana</i>

Table 1. The *Erythrodiplax connata* group, according to Borror, 1942, and the present study.

As construed by Borror (1942), the subspecies *Erythrodiplax c. connata* had a peculiarly disjunct distribution, occurring from Arizona and Texas in the United States to Jalisco in southern Mexico and again in Chile and western Argentina. Borror also cited specimens from Cuba, Jamaica, Ecuador, and Peru, but it is unlikely that any of them were actually *connata* (see below). Further examination of specimens makes it clear that the two very isolated populations of "*E. c. connata*" are distinct from one another, in fact a southern species restricted to Chile and Argentina and a northern species restricted to the uplands of southwestern United States and the Mexican Plateau and the lowlands of western Mexico. As Chile is the type locality of *connata*, that name is restricted to the southern species, which occurs from Coquimbo south to Palena in Chile and in Chubut Province in southwestern Argentina.

The northern "*E. c. connata*" is sufficiently different to warrant species status; thus it needs a name. It appears to be restricted to Mexico and southwestern United States, and the only other name applied to a population of the *connata* group within that range is *Trithemis basifusca* Calvert (1895) from Baja California; thus it must be called *Erythrodiplax basifusca* (Calvert, 1895). Calvert (1899) reported *basifusca* from Tepic, Mexico, and further (1901-1908) from Costa Rica, Brazil, and

Paraguay. The species described from Baja California certainly does not occur in the last three countries, and this is justification to reassess all previously published records of distribution of species of this group.

These two species differ primarily in abdomen width (Table 2, Figure 1), and the difference is consistent and non-overlapping. Borror (1942: 13) noted this when he wrote of the genus "abdomen usually slender and cylindrical, occasionally (*connata connata* from Chile) somewhat flattened dorsoventrally." Relatively broad abdomens may characterize species of the cool Chilean mountain and forest region, perhaps for thermoregulatory reasons; *Aeshna diffinis* Rambur of that region has a broader abdomen than the very closely related *A. absoluta* Calvert of the lowlands and dry uplands of Argentina (von Ellenrieder 2001). In addition, the tibiae of mature female and many mature male *basifusca* are pale brown on the outer surface, those of mature male and female *connata* always black. The outer surface of the femur has a narrow yellow stripe in female *connata* but is extensively yellow in female *basifusca*. Finally, there is a slight average difference in abdominal pruinosity in males. In *basifusca*, pruinosity extends back to segment 6 or 7, in *connata* to segment 7 or 8.

SPECIES	N	RELATIVE WIDTH OF SIXTH ABDOMINAL SEGMENT					
		0.45-0.50	0.51-0.55	0.56-0.60	0.61-0.65	0.66-0.70	0.71-0.75
<i>abjecta</i>	5		3	2			
<i>basifusca</i>	6	2	1	3			
<i>connata</i>	11				5	4	2

Relative width = width of one side of dorsal tergum at posterior end of segment / total length of segment

Table 2. Comparison of abdomen width in males of 3 species of *Erythrodiplax*.

NORTHERN POPULATIONS OF THE CONNATA GROUP; CONFUSION BETWEEN *E. BASIFUSCA* AND *E. ABJECTA*

Much confusion was generated by Borror's (1942) considering *basifusca* as a synonym of *Erythrodiplax abjecta* (Rambur), a species that does not occur in northern Mexico. Muttkowski (1910) listed *basifusca* as a subspecies of *E. connata*, and Ris (1911) listed it as a synonym of *E. connata abjecta*, with additional records from Putla and Cuernavaca, Mexico (*abjecta* does not occur at those localities, although *basifusca* surely does). Borror (1942) raised *abjecta* to species level, and *basifusca* has remained a synonym of *abjecta* since that time. Borror listed specimens of *E. abjecta* from Baja California, probably following Calvert (1899), Ris (1911), and Williamson and Williamson (1930) in considering this population as representing *abjecta*. Because it occurs south at least to Colombia (the type locality) and Venezuela, *abjecta* has generally been considered to coexist widely with "*E. c. connata*" in Mexico. The latter was listed by Borror from Nayarit, Morelos, Michoacan, and Jalisco, and all these records doubtless refer to *basifusca*.

As neither Borror (1942) nor I examined the type of *abjecta* from Colombia, the application of this name to a particular species may be in doubt, but Borror interpreted Ris's (1911) description of the type in applying that name to a species that occurs from northern South America north through the uplands of Costa Rica to Chiapas, Mexico, and I am following his lead here. The two species are much alike and could not be distinguished in the field, but in fact most members of the *connata* group are very similar to one another, which has led to continued confusion up to the time of Borror and beyond. Both *abjecta* and *basifusca* are dark species with blue-black frons and blue abdominal pruinosity in mature males. They can be distinguished primarily by penis shape (Figure 2).

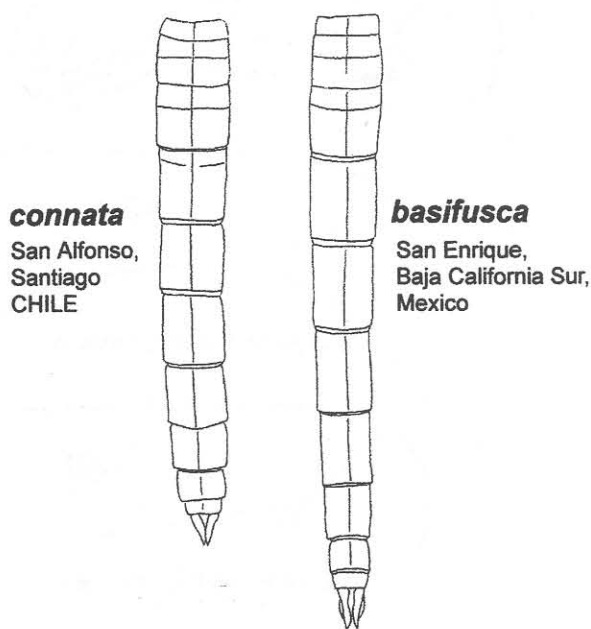


Figure 1. Dorsal view of abdomen of typical male specimen of *Erythrodiplax connata* and *E. basifusca*.

The penis of *abjecta* is slightly longer and more slender than that of *basifusca*, has a less expanded tip, lacks an apical tubercle, and has a more strongly projecting median process. In *abjecta*, the distalmost point on the second segment of the penis (not including the median process) is at the base of the median process, while in *basifusca*, the distalmost point of that segment is at the apical tubercle, dorsal to the base of the median process. The penis of *E. connata* appears identical to that of *E. basifusca*. About the penis of *E. abjecta*, Borror (1942: 190) wrote "the apical tubercle is lacking, except in the specimen from Lower California, where it is faintly indicated." That

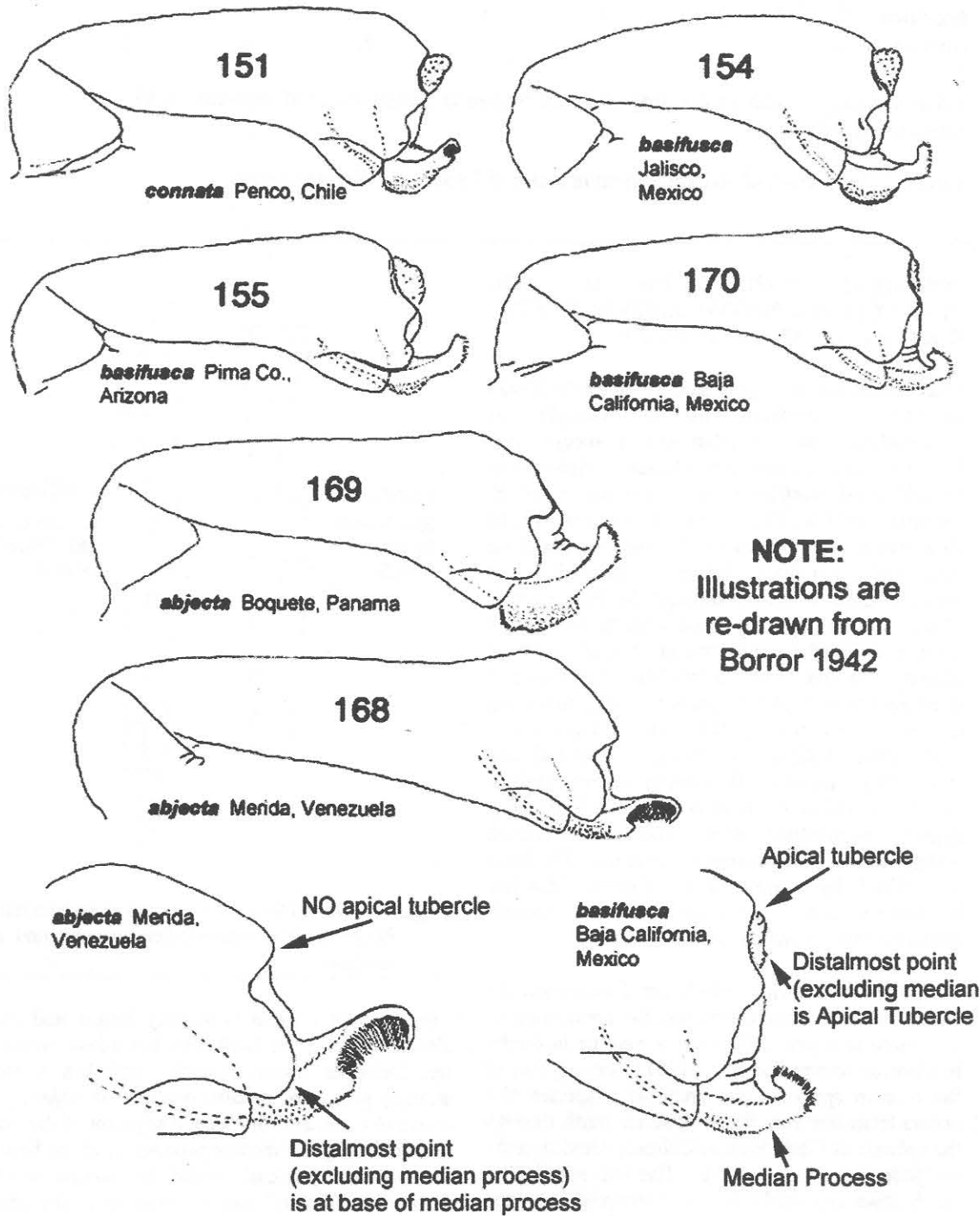


Figure 2. Drawings of penes of species of the *Erythrodiplax connata* group taken from Borror (1942) Numbers refer to Borror's original figures.

specimen is illustrated in Figure 2. Borror based his assessment of the Baja California population as *abjecta* on this single specimen, and in fact, recent specimens from Baja California have well-developed apical tubercles.

Examination of one of the syntypes of *Trithemis basifusca* Calvert from the Museum of Comparative Zoology has cleared up the confusion, as indeed it is a member of the northern species that occurs from Arizona and Texas to Oaxaca. Although relatively large and with extensive color at the wing base, it matches the northern species rather than *abjecta* in penis length and structure and hamule structure. I am herein designating this specimen as the lectotype of *T. basifusca*. It is specimen 8840, in quite good condition, pinned and with the following tags: (1) Mesa Verde, Baja Cal., Oct. 1893, male, G. Eisen, P. P. Calvert; (2-red) Type 8840; (3) *Trithemis basifusca* Calvert, male Type. Face dark metallic blue; thorax and abdominal segments 1-2 dark reddish-brown; abdominal segments 3-6 pruinose blue dorsally, 7-10 black, cerci and epiproct dark yellow; legs black, femora of first two pairs light brown basally; pterostigmas yellow; brown hindwing spot extends out to first antenodal, halfway between anal crossing and inner edge of triangle, and innermost cell of first row of anal loop, and extends back just over half the wing width at base. Forewing antenodals 9-1/2/10, postnodals 8/7; hindwing antenodals 8/8, postnodals 7/7. Abdomen 22 mm, hindwing 25.5 mm.

On the average, *abjecta* is slightly larger (male hindwing mean 25.8 mm, range 24-28, N=10) than *basifusca* (male hindwing mean 23.2, range 21-26, N=15), has slightly more color at the wing base (*abjecta* has a very dark brown spot usually extending posteriad almost even with the heel of the anal loop, and *basifusca* has a lighter brown spot often not extending posteriad of the anal vein), and has the inner branch of the hamules relatively longer, but all of these characters overlap. Three male *basifusca* from lowland Sinaloa and Sonora have basal wing spots much like those of typical *abjecta*, while those spots are intermediate in three others from the same area. However, all highlands *basifusca* examined have spots smaller and paler than all *abjecta* examined. The hindwing spot in male *connata* is dark and is intermediate between typical *basifusca* and typical *abjecta* in extent.

THE STATUS OF *ERYTHRODIPLAX FUSCA* AND *E. MINUSCULA* AND THE *CONNATA* GROUP IN NORTH AND MIDDLE AMERICA

Garrison (1991) suggested that *E. fusca* and *E. minuscula* should be considered full species, as the red-faced *E. fusca* occurs between the blue-faced *connata* (= *basifusca*) and *minuscula*, and there appeared to be no intergrades between them, contrary to Borror's assertions. I concur with Garrison, as there are several lines of evidence indicating they are not conspecific, including the lack of intergrades among the material examined by me. Borror's (1942: 170) claim for conspecificity of *minuscula* and *connata* was the "intergradation of this form [*minuscula*] with the *connata connata* [= *basifusca*] from southwestern United States and Mexico," but in fact he cited no specimens of the two forms between Louisiana and western Texas, a very large gap. As presently known, *E. basifusca* occurs east to Brewster County and *E. minuscula* west to Bexar County, Texas (J. Abbott, pers. comm.), the gap between them about 500 kilometers. Furthermore, a dramatic difference in coloration exists between the two species. Male *E. basifusca* develop pruinosity only on the third to seventh abdominal segments, while male *E. minuscula* become pruinose all over the thorax and abdomen to the seventh segment (*E. paraguayensis* appears to be the only other species of the group colored like this).

Similarly, the tropical red-faced species *E. fusca* stands out as distinct from all blue-faced species of this group because of its coloration. There are now records of *E. fusca* in Blanco, Edwards, Frio, and Medina counties, Texas (J. Abbott, pers. comm.; D. Paulson, pers. obs.), between the known ranges of *E. basifusca* and *E. minuscula*. Although the range of *fusca* approaches that of *minuscula* very closely, no intermediate specimens have been found, and with further field work, the two species might be found in sympatry.

E. basifusca occurs at sea level in Baja California and not far above it in Sinaloa, but it occupies ever higher elevations toward the south, and the lowest elevation from which I have seen it in southern Mexico is 1128 meters near Tamazula, Jalisco. Calvert (1899) recorded it from Tepic, Nayarit, the elevation of which is about 1000 meters. The highest I have seen *fusca* in Mexico is 1460 meters near Tehuacán, Puebla, and 1130 meters in central Chiapas. I know of only one record of sympatry of any member of the group in



Figure 3. Ranges of some blue-faced species of the *Erythrodiplax connata* group.

Mexico, at a rain pond at km 49 (4 km S Tehuacán exit) on Oaxaca-Mexico Autopista, 1460 meters, where I took two male *fuscus* and one male *basifusca* on 23 September 1999 and saw additional males of each species. At this locality, not only was the difference in frons color obvious, but the two *basifusca* seen were slightly larger than the half-dozen *fuscus* seen, with distinctly less dark coloration in the wing base. The three specimens show no sign of intergradation. Additional collecting may bring to light other instances of sympatry of these two species.

The distribution of the three members of the *connata* group in Mexico is thus largely allopatric, with *fuscus* a wet lowland species occurring north to Colima on the west coast and Tamaulipas on the east coast (González Soriano and Novelo Gutiérrez 1996), *basifusca* a dry west coast and highlands species occurring at low elevations south to Sinaloa and on the Plateau south to Oaxaca, and *abjecta* a wet highlands species occurring in Chiapas from

1520 to 2260 meters. The Isthmus of Tehuantepec presumably acts as a lowland barrier between the two highland species.

In Costa Rica, two species of the group are common, *E. abjecta* in the highlands (800 to 1430 meters) and *E. fusca* in the lowlands (up to 1220 meters). *E. abjecta* was common near San Vito de Java, Puntarenas Province, from 1000 to 1400 meters, *E. fusca* similarly common from 1000 to 1220 meters, and both were collected at a small pond at the San Vito airport at 1070 meters. Also, *E. abjecta* was common at a marsh at Tapantí, Cartago Province, at 1190 meters elevation, and I saw an unmistakable red-faced male *E. fusca* there on one visit. Thus the two are sympatric and syntopic in Costa Rica with no sign of interbreeding.

THE *CONNATA* GROUP IN SOUTH AMERICA

Borrer stated that the specimens of *connata connata* he examined from Peru northward had relatively slender abdomens, and therefore they cannot be *connata* as restricted here. He also mentioned specimens from Mendoza Province in western Argentina with slender abdomens and relatively small basal spot in the hindwing; these also were probably not *connata* and may have been the same as a species that is known from farther north in the Andes of Argentina that is either an undescribed species or a high-elevation representative of *E. fusca*. The latter is common throughout the tropical lowlands of South America (see Appendix 1).

Other species in the *connata* group that occur in South America are *E. abjecta*, *E. cauca*, *E. cleopatra* Ris, *E. media* Borrer, and *E. melanorubra* Borrer. The first two are restricted to the northern Andes. I consider the first four species not conspecific with *connata* because all are

slender-bodied and not conspecific with *fusca* because all have purple to blue frons. Of the species that occur near the range of *E. connata*, both *cleopatra* and *media* have pale outer tibial surfaces when mature, unlike *connata*. *E. cleopatra*, restricted to the arid coast of Peru and far northern Chile, is probably the source of published records of *connata* from Peru and perhaps Bolivia; it is not sympatric with any other species of the group. *E. media* is restricted to the lowlands of southern Brazil, extending just into eastern Bolivia, Paraguay, and northern Argentina, and is not known to approach the montane range of *connata*; it is widely sympatric with *fusca*, however. *E. melanorubra* is also slender-bodied but has a reddish frons like *fusca*; it is larger than *fusca*, with a relatively longer and more slender penis. It is also a lowland species and widely sympatric with *fusca* in South America, but it appears to be much less common.

THE *CONNATA* GROUP IN THE WEST INDIES

In the West Indies, the situation has long been confused because of published records of *connata* from these islands (Borror 1942, Whitehouse 1943, Paulson 1966). Borror (1942: 174) wrote of *E. connata connata* that "the material from the West Indies tends to intergrade with *connata minuscula* from southeastern United States," thus attributing to these dragonflies gene flow greater than I expect from them. The record by Paulson (1966) of *connata* from the Bahamas was retracted by Paulson (1982) as a misidentification. The record by Whitehouse (1943) from Jamaica is based on teneral specimens, which are very difficult to allocate to species in this group. Their identity remains a mystery, but they are probably not *connata* as defined herein. Probably only two described species of the *connata* group occur in the West Indies, the widespread *E. justiniana* (Selys) and the poorly known *E. bromeliicola* Westfall.

E. justiniana is easily distinguished from the other members of the group by a combination of blue frons, small size, and large basal wing markings in the male. With the restriction of *connata* to southern South America, two of its synonyms (*Diplax fraterna* Hagen, 1873, and *Diplax portoricensis* Kolbe, 1888) must be removed from that synonymy. *D. fraterna* cannot be assigned to any known species, the description being nothing more than Hagen's (1873) assigning that name to two specimens in the Scudder collection. Although Borror lists the type locality

as "West Indies," Hagen was clearly referring to specimens from Cuba in his discussion, so the type locality of *fraterna* should be restricted to Cuba. Also, Borror listed the original reference as page 376, when it is in fact page 375, under the discussion of *E. ochracea*. Borror was apparently unable to locate Hagen's types of this species, and I consider the name *fraterna* a nomen nudum.

Ris (1911) did not examine specimens of *E. portoricensis*, described from Puerto Rico, but questionably synonymized it with *E. minuscula*, which he thought ranged into South America. Borror (1942) synonymized it instead with *E. c. connata*, and I suspect he did so merely because it could not be a synonym of *minuscula* because of geography, so he placed it with the subspecies of *connata* he considered to inhabit the West Indies. *E. portoricensis* is very likely a synonym of *E. justiniana*, the only member of the group known to occur in Puerto Rico.

Those West Indian records not attributable to *justiniana* probably involve *E. bromeliicola*, a species of the Greater Antilles (Needham, Westfall, and May 2000) that is readily distinguishable from other members of this group. The species is definitely known from Jamaica and Cuba but may occur on other islands. M. J. Westfall, Jr. (pers. comm.) examined one of the specimens listed from Jamaica as *connata* by Borror (1942) and found it to be this species.

However, I examined a single specimen of the *connata* group from San Diego de los Baños, Cuba, that is not *justiniana* and does not seem to be *bromeliicola*. If correctly labeled and not merely an extreme variant of *bromeliicola*, it indicates the presence of another member of this group in the West Indies, but I cannot definitely associate it with any of the mainland species.

KEY TO SPECIES

This key can be used only for males, as females of many of the species are inseparable. Furthermore, knowledge of the place of origin of a specimen is essential for distinction of very similar species. Penis morphology is distinctive for many of the species, but this character has been used only when absolutely necessary.

1	Hindwing length ≤ 20 mm; mature male with pruinose thorax	2
1'	Hindwing length > 20 mm (except one species from West Indies); mature male with no pruinosity on thorax.....	3
2	Terminal appendages dark; South America	<i>paraguayensis</i>
2'	Terminal appendages pale; North America	<i>minuscula</i>
3	Wing tips dark brown or black	<i>atroterminata</i>
3'	Wing tips clear	4
4	Face dark red (may be purplish-red in specimens)	5
4'	Face dark blue to purplish-blue	8
5	Abdomen red, without pruinosity	<i>fusca</i>
	(certain Central and South American populations)	
5'	Abdominal segments of mature male with	6
6	Terminal segment of penis > 1.4 mm in length; basal spot in hindwing small, triangular, extends at most to second antenodal	<i>melanorubra</i>
6'	Terminal segment of penis < 1.3 mm in length; basal spot in hindwing typically larger, rounded, extends usually past second antenodal but much variation	7
7	Abdominal pruinosity extends onto segment 9; mountains of western Argentina	cf. <i>fusca</i>
7'	Abdominal pruinosity extends only onto segment 7; lowland tropics	<i>fusca</i>
8	Hindwing with prominent basal spot extending to triangle and anal angle	9
8'	Hindwing with virtually no coloration, if a spot then not reaching triangle or anal Angle	10
9	Hindwing length > 25 mm; South America	<i>ines</i>
9'	Hindwing length < 25 mm; West Indies	<i>justiniana</i>
10	Abdomen black, thorax with yellow middorsal stripe; West Indies	<i>bromeliicola</i>
10'	Abdomen pruinose blue; thorax without such a stripe; mainland	11
11	Abdomen relatively thick (width of one side of dorsum of segment 6/length of segment > 0.61); temperate zone of Chile and southern Argentina	<i>connata</i>
11'	Abdomen more slender (same measurement ≤ 0.60); occurring elsewhere	12
12	Terminal segment of penis < 1.3 mm in length; northern Argentina and eastern Bolivia east across southern Brazil	<i>media</i>
12'	Terminal segment of penis > 1.3 mm in length; not in that geographic area	13
13	Thorax of mature male black; hindwing spot barely reaches first antenodal; coastal lowlands of northern Chile and Peru	<i>cleopatra</i>
13'	Thorax of mature male with reddish-brown tones; hindwing spot extends beyond first antenodal; not in that geographic area	14
14	Oaxaca, Mexico, and northward	<i>basifusca</i>
14'	Chiapas, Mexico, and southward	15
15	Penis with apical tubercle; known only from Colombia	<i>cauca</i>
15'	Penis without apical tubercle; Ecuador north to Chiapas	<i>abjecta</i>

DISCUSSION

The *Erythrodiplax connata* group represents a cluster of very similar and presumably relatively recently derived species. A core group of *abjecta*, *basifusca*, *cleopatra*, *connata*, *fusca*, *media*, *melanorubra*, and *minuscula* includes species that are mostly allopatric to one another, and their habitat preference of marshy ponds and slow streams seems identical wherever they occur. Females of this group are virtually indistinguishable from one another. Males differ in frons color and extent of pruinosity in mature males, abdomen width, and penis structure. Brown markings at the

base of the hindwings differ in extent on the average but with much overlap.

Notwithstanding their similarities, I consider the species in this group distinct entities, most of them restricted to specific biogeographic regions (see Appendix 1, Figure 3). *E. fusca* is the very widespread tropical lowland species, occurring from southern Texas to northern Argentina and extending up to middle elevations in many mountain ranges. It is replaced in the wet temperate lowlands of southeastern United States by *E. minuscula*; at higher elevations and in drier regions of Mexico by *E. basifusca*; at higher elevations in

Central and northern South America by *E. abjecta*; on the arid Pacific lowlands of South America by *E. cleopatra*; and south of that at the cool, wet southern end of South America by *E. connata*.

Although populations in the northern Argentinean Andes look very similar to *fusca*, I consider them probably a distinct species, as they have much less brown in the hindwing base than typical *fusca* (although overlapping with the least-marked individuals of that species), and the abdominal pruinosity of males extends from the third to the ninth segment, while it is limited to the third to seventh segment in *fusca*. In addition, these populations are associated with a higher, drier climatic zone than *fusca* inhabits elsewhere. A collecting transect between the ranges of *fusca* and its montane relative in Argentina is needed.

Two species of the group appear to be widely sympatric with *E. fusca* in the South American lowlands: *E. media* in southern South America and *E. melanorubra* over a considerably larger area. *E. media* is similar to *abjecta*, *basifusca*, and *cleopatra* in having a blue frons and slender abdomen but is isolated from all of them in a very different climatic region. *E. melanorubra* remains enigmatic in its wide sympatry with the superficially similar but smaller *E. fusca*; ecological differences between the two species, if any, are yet to be elaborated. If *E. cauca*, so far known from only the Cauca Valley of southwestern Colombia, is sympatric with *E. abjecta*, this would be the only instance of sympatry between two species of this group so similar that they could not be distinguished on the basis of appearance.

Obvious color differences occur only in the face, with blue- and red-faced species. Males of all species develop pruinosity on the abdomen with maturity, with the exception of at least some populations of *E. fusca*. These red-abdomened males of *E. fusca* occur from the southern Pacific side of Costa Rica to western Ecuador and in southern Brazil, usually not sympatric with the blue-abdomened type. I have insufficient samples to determine further occurrence. They seem to differ in no other way from typical *fusca*, but the two color types should be compared in the event of future molecular studies.

Penis length varies but does not distinguish many of the species; it does differentiate the members of two very similar species pairs, *fusca* from *melanorubra* and *abjecta* from *basifusca*. The significance of differences in penis structure

remains unknown, although there may be a tendency for genitalic structures to diverge rapidly as populations become genetically isolated, as they are not constrained by ecological factors (M. McPeck, pers. comm.).

Although the species of this group seem to be very similar to one another in their habitat selection and general behavior, field studies may show more differences in life style than are now apparent. A molecular phylogenetic analysis of the group would be of great interest.

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Appendix 1. Specimens of *Erythrodiplax* examined for this study. Specimens examined totaled 855, comprising 423 records, and they are summarized here to save space. A complete list is available from the author. The total number of males and females is indicated, then the number from each country, with states and provinces from which specimens were examined listed in parentheses.

E. abjecta 43-5; Costa Rica 35-2 (Alajuela, Cartago, Puntarenas, San José), Ecuador 4-0 (Pichincha), Mexico 2-3 (Chiapas), El Salvador 1-0 (Metapan), Venezuela 1-0 (Mérida).

E. basifusca 46-11; Mexico 35-10 (Baja California Sur, Durango, Jalisco, Michoacan, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Sonora), USA 11-1 (Arizona, New Mexico).

E. bromeliicola 9-16; Cuba 5-10 (Isla de Juventud, Oriente, Pinar del Rio), Jamaica 4-6 (Manchester, St. Ann, St. Thomas).

E. cleopatra 11-17; Chile 1-2 (Camarones), Peru 10-15 (Arequipa, La Libertad, Lima).

E. connata 37-15; Argentina 3-1 (Chubut), Chile 34-14 (Contulmo, Coquimbo, Curico, Linares, Llanquihue, Nuble, O'Higgins, Palena, Peillem-Pille, Santiago, Valparaiso).

E. fusca 345-138; Argentina 3-4 (Buenos Aires, Misiones), Belize 6-0 (Cayo), Brazil 19-7 (Goias, Sao Paulo), Colombia 29-4 (Chocó, Tolima, Valle), Costa Rica 129-34 (Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, San José), Ecuador 20-11 (Esmeraldas, Napo, Pichincha), Guatemala 18-9 (Huehuetenango, Izabal, Petén, Solola, Suchitepequez), Honduras 8-8 (Cortez, Francisco Morazán, Mosquitia), Mexico 37-16 (Campeche, Chiapas, Colima, Oaxaca, Puebla, San Luis Potosí, Tabasco, Tamaulipas, Veracruz, Yucatan), Panama 4-0 (Canal Zone, Colón, Panama), Paraguay 1-0 (Amambay), Peru 50-38 (Huanuco, La Libertad, Loreto, Madre de Dios, Pasco), El Salvador 2-0 (Libertad), Trinidad 4-0 (St. Andrew, St. George), USA 0-1 (Texas), Venezuela 15-6 (Amazonas, Aragua, Guárico).

E. cf fusca 15-8; Argentina 15-8 (Catamarca, Jujuy, Salta, Santiago del Estero, Tucumán).

E. justiniana 12-8; Bahamas 1-0 (Andros), Cuba 1-0 (Las Villas), Haiti 2-2 (Sud), Jamaica 3-0 (St. Andrew, St. Catherine), Puerto Rico 5-6.

E. media 18-2; Argentina 1-0 (Jujuy), Bolivia 1-0 (Santa Cruz), Brazil 13-0 (Rio Grande do Sul, Santa Catarina, Sao Paulo), Paraguay 3-2 (Chaco).

E. melanorubra 4-0; Argentina 1-0 (Misiones), Ecuador 2-0 (Napo, Santiago Zamora), Peru 1-0 (Ayacucho).

E. minuscula 54-32; USA 54-32 (Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Texas).

E. paraguayensis 6-3; Argentina 1-0 (Misiones), Bolivia 1-1 (Santa Cruz), Paraguay 2-2 (Central, Guaira, San Pedro Cororo), Venezuela 2-0 (Bolívar).

BULLETIN OF AMERICAN ODONATOLOGY

VOLUME 4

AN ANNOTATED LIST OF THE ODONATA OF NEW JERSEY

With an Appendix on Nomenclature in the Genus *Gomphus*

Michael L. May & Frank L. Carle 4(1): 1 - 35

THE ODONATA OF PATUXENT WILDLIFE RESEARCH CENTER AND VICINITY,

Richard L. Orr 4(2): 37 - 67

THE STATUS OF *LESTES APOLLINARIS* NAVÁS AND *L. HENSHAWI* CALVERT,

Thomas W. Donnelly 4(3): 69-74

THE DRAGONFLIES OF WASHINGTON, Dennis R. Paulson 4(4): 75-90

VOLUME 5

THE DRAGONFLIES AND DAMSELFLIES (ODONATA) OF LOUISIANA, Bill Mauffray

5(1): 1-26

ODONATA OF THE CAYMAN ISLANDS: A REVIEW, R. R. Askew, Richard Prosser, and

Philip S. Corbet 5(2): 27-32

TAXONOMIC AND POPULATION STUDIES OF BRITISH COLUMBIA *AESHNA*

SPECIES, G. Peters 5(2): 33-42

ADAPTING THE TOWNES MALAISE TRAP FOR COLLECTING LIVE ODONATA,

Robert C. Glotzhober & Dan Riggs, 5(3): 43-48

***ARCHILESTES GRANDIS* (GREAT SPREADWING) IN CENTRAL NEW JERSEY, WITH**

NOTES ON WATER QUALITY, David P. Moskowitz and David M. Bell, 5(3): 49-54

VARIATION IN HEAD SPINES IN FEMALE *OPHIOGOMPHUS*, WITH A POSSIBLE

EXAMPLE OF REPRODUCTIVE CHARACTER DISPLACEMENT (ANISOPTERA:

GOMPHIDAE), Dennis R. Paulson, 5(3): 55-58

THE ODONATA FAUNA OF CONNECTICUT, David L. Wagner and Michael C. Thomas,

5(4): 59-85

VOLUME 6

THE DISTRIBUTION OF THE ODONATA OF HAWAII , Jerrell J. Daigle, 6(1): 1 - 5

ADDITIONS TO THE DESCRIPTION OF *GOMPHOMACROMIA NODISTICTA* RIS, 1928

(ANISOPTERA: CORDULIIDAE), N. von Ellenrieder, 6(1): 7-11

THE ODONATA OF IOWA, Robert W. Cruden and O. J. Gode, Jr., 6(2)p. 13-48

ODONATA IN THE GREAT PLAINS STATES: PATTERNS OF DISTRIBUTION AND

DIVERSITY, Roy J. Beckemeyer, 6(3) p. 49-99

COMMENTS ON THE *ERYTHRODIPLAX CONNATA* (BURMEISTER, 1839) GROUP,

WITH THE ELEVATION OF *E. FUSCA* (RAMBUR, 1842), *E. MINUSCULA* (RAMBUR,

1842), AND *E. BASIFUSCA* (CALVERT, 1895) TO FULL SPECIES (ANISOPTERA:

LIBELLULIDAE), Dennis Paulson, 6(4) p. 101-110

BULLETIN OF AMERICAN ODONATOLOGY

VOLUME 1

THE ODONATA OF NEW YORK, Thomas W. Donnelly 1(1): 1-27

DISTRIBUTION OF DRAGONFLIES AND DAMSELFLIES (ODONATA) IN FLORIDA, Sidney W. Dunkle 1(2): 29-50

MORPHOLOGICAL AND ECOLOGICAL DIFFERENCES AMONG SPECIES OF *LADONA* (ANISOPTERA: LIBELLULIDAE), Michael L. May 1(3): 51-56

COMPORTAMIENTO REPRODUCTIVO Y POLICROMATISMO EN *ISCHNURA DENTICOLLIS* Burmeister (Zygoptera: Coenagrionidae), [Reproductive behavior and polychromatism in *Ischnura denticollis*], with English summary Alejandro Córdoba Aguilar. 1(3): 57-64

A CHECKLIST OF THE ODONATA OF THE DOMINICAN REPUBLIC BY PROVINCE, Jerrell James Daigle 1(4):65-69

ODONATA DE LA SIERRA DE HUAUCHINANGO, PUEBLA, MEXICO [Odonata of the Sierra de Huachinango, Puebla, Mexico], José A. Gómez Anaya y Rodolfo Novelo Gutiérrez 1(4):71-73

VOLUME 2

LA NAYADE DE *ARCHILESTES LATIALATUS* DONNELLY, 1981 (ZYGOPTERA: LESTIDAE) [The naiad of *Archilestes latialatus* Donnelly, 1981], R. Novelo-Gutiérrez 2(1): 1-7

DESCRIPCIÓN E HISTORIA NATURAL DE LAS LARVAS DE ODONATOS DE COSTA RICA. I II: *GYNACANTHA TIBIATA* (KARSCH 1891) (ANISOPTERA, AESHNIDAE) [Description and Natural History of of the Odonata Larvae of Costa Rica. III: *Gynacantha tibiata* (Karsch 1891)(Anisoptera: Aeshnidae)], Alonso Ramírez 2(1): 9-14

DESCRIPTION OF THE NYMPH OF *EPITHECA (TETRAGONEURIA) SPINOSA* (HAGEN) (ODONATA:CORDULIIDAE), K. J. Tennessen 2(2): 15-19

THE LARVA AND ADULT MALE OF *SOMATOCHLORA GEORGIANA* WALKER (ODONATA: CORDULIIDAE), Jerrell J. Daigle 2(2): 21-26

MACROMIA ILLINOIENSIS AND *GEORGINA*: A STUDY OF THEIR VARIATION AND APPARENT SUBSPECIFIC RELATIONSHIP (ODONATA: CORDULIIDAE), Thomas W. Donnelly and Kenneth J. Tennessen 2(3): 27-61

THE SUBGENUS *TETRAGONEURIA* (ANISOPTERA: CORDULIIDAE: *EPITHECA*) IN NEW JERSEY, Michael L. May 2(4): 63-74

VOLUME 3

THE ODONATA OF OHIO - A PRELIMINARY REPORT, Robert C. Glotzhober 3(1): 1 - 30

FOUR DECADES OF STABILITY AND CHANGE IN THE ODONATA POPULATIONS AT TEN ACRE POND IN CENTRAL PENNSYLVANIA, Clark N. Shiffer and Harold B. White 3(2): 31 - 41

DESCRIPCION E HISTORIA NATURAL DE LAS LARVAS DE ODONATOS DE COSTA RICA. IV: *MECISTOGASTER ORNATA* (RAMBUR, 1842) (ZYGOPTERA, PSEUDOSTIGMATIDAE). [Description and Natural History of Odonata larva of Costa Rica. IV. *Mecistogaster ornata* (Rambur, 1842) (Zygoptera, Pseudostigmatidae)], Alonso Ramírez 3(2): 43-47

THE DISTRIBUTION OF ODONATA IN ALABAMA, Kenneth J. Tennessen, James D. Harper, R. Stephen Krotzer, 3(3): 49-74

DISTRIBUTION RECORDS OF THE ODONATA OF MONTANA, Kelly B. Miller and Daniel L. Gustafson, 3(4): 75 - 88 continued on inside cover