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BY

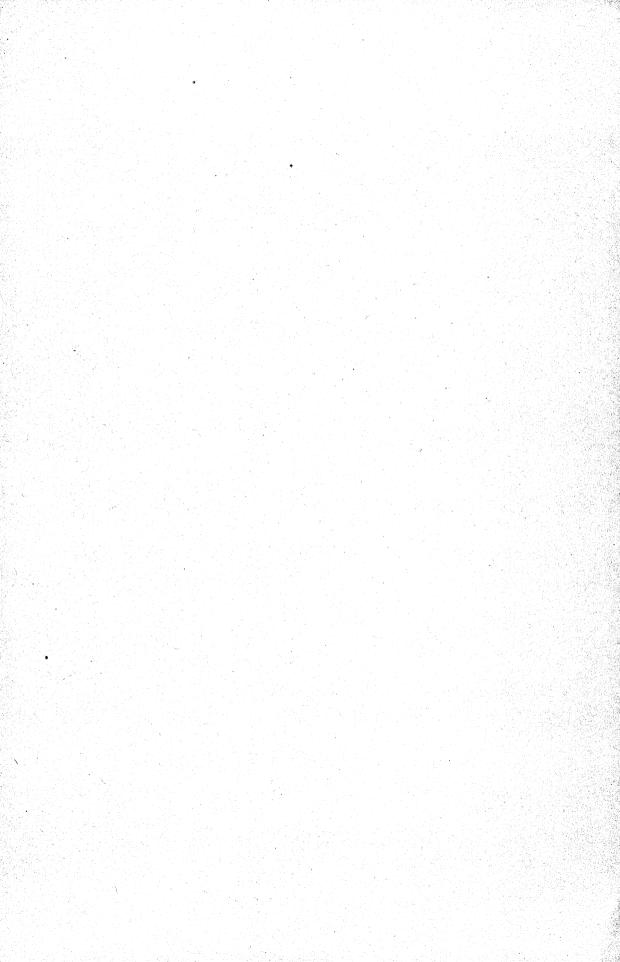
E. B. WILLIAMSON

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CLARENCE HAMILTON KENNEDY

ANN ARBOR, MICHIGAN PUBLISHED BY THE UNIVERSITY JULY 14, 1923



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> ALEXANDER G. RUTHVEN, Director of the Museum of Zoology, University of Michigan.

NOTES ON THE GENUS ERYTHEMIS WITH A DESCRIPTION OF A NEW SPECIES (ODONATA)

By E. B. Williamson

This paper discusses in a general way the distribution of the species of the genus and some possible factors involved, recording specimens taken in the Canal Zone, Panama, Colombia, and Venezuela,¹ the genus is defined, following earlier authors; a key to the species, based on some characters heretofore used and on some new characters, and therefore supplementary to keys by Calvert and Ris, is given; and a new species, the first to be recognized as such in this genus for many years, is described. The paper deals only with imagos.

A GENERAL CONSIDERATION OF THE DISTRIBUTION OF THE SPECIES OF ERYTHEMIS

A reference to the literature, summarized by Ris in Coll. Zool. de Selys, will reveal at once the wide distribution of the species of this genus. For example, seven of the eight known species occur in the West Indies, yet none is peculiar there, and of the seven species, five have each a range at least from Mexico to Paraguay. These dragonflies have been generally successful in passing over or around whatever obstacles the varied topography of tropical America could offer to their dispersal.

Dragonflies as larvae and adults are active and more or less independent of any one particular source of food. The larvae are aquatic and are hence dependent on some water supply. The adults are on the wing when they seize their food, and hence can sustain themselves only under certain weather conditions which are equally important for mating and ovipositing. In conformity with the complexities of multiform bodies of water under diverse climatic conditions, we find equally complex adjustments of dragonflies to meet varying conditions. Regions with pronounced seasons, involving changes in precipitation or temperature or both, and dry or frigid regions, have relatively fewer species of dragonflies than tropical regions with a more uniform climate and an abundant water supply throughout the year. In eastern North America the broad belt of dragonfly fauna bounded on the south by the northernmost extension of such genera as Dythemis, Orthemis, Brachymesia, and Neoneura, for example, and on the north by Cordulia, Agrion, and the bulk of Somatochlora and Aeshna, for example, is probably confined to its area and protected from encroachments from the south and north largely by the temperature factor in the climate.

Directly associated with the adjustments of dragonflies to seasonal changes is their dependence on the orderly sequence of these seasons. Hence, in any

¹ See first paragraph, Misc. Publ., Mus. of Zoology, University of Michigan, No. 9.

region of marked seasonal changes there are more or less frequent changes in the dragonfly fauna of various habitats due to unusual or abnormal seasons. It is obvious that the premature drying up of a pond might result in the death of the larvae of several species. An unusually high water stage of a river might submerge all the resting places for emerging larvae at the time when they are due to emerge, or might coat larvae with a deposit of stiff clay, resulting in the wholesale destruction of many species. Late frosts in early summer or a premature freeze in the fall might cause the death of imagoes and thus at least temporarily eliminate certain species from certain habitats. Unusual seasons may also operate to the advantage of certain extralimital species. For example, an early and continuously warm spring may permit the extension northward of a southern species, and it is probably this factor, associated possibly also with favorable air currents, that sometimes carries the southern *Pantala hymenaea* as far north as Ontario.

In the low-lying American tropics temperature ceases to be an important factor in itself in determining dragonfly distribution. Drought takes its place. Drought makes itself felt even in the well-watered and forested equatorial belt, though, due to permanent rivers and lakes, its effect is not universal over a region as low temperature is. It is obvious, with low temperature absent as a limiting factor in the seasonal distribution of dragonflies, at least as imagoes, that more numerous adjustments in other factors are possible in the life histories of these insects. For example, in the north the rigors of winter can be bridged by a dragonfly only in the egg or larval stage, but in the tropics it is not impossible that the period of drought might be passed as an egg, a larva, or an imago. The existence in the tropics of both temporary and permanent bodies of water have resulted in many diverse adjustments in the life histories of dragonflies, both as larvae and imagoes, to these periods of drought. For example, warmth and abundant food obviously might permit the shortening of larval life, while other factors might permit the indefinite extension of imaginal life. When, as is usually the case, temporary and permanent bodies of water occur in close proximity in a region, the result is a rich and varied dragonfly fauna.

It is interesting to note that in the tropics many of the most successful and specialized dragonflies are those which depend on, or are able to endure, a temporary water supply (wet weather ponds or streams) for their larval life, and that in the north our highly specialized species are pond and lake (not stream) dwellers.

Too little is known of the detailed life histories of neotropical dragonflies to allow us to cite particular examples of the various adjustments indicated as possible in the preceding paragraphs. This is true of the species of Erythemis, and yet enough is known to permit of a few positive statements and some warranted conclusions. The larvae of the species of Erythemis, so far as known, are pond or lake dwellers, always so, possibly, in the case of some species, and frequently or usually in the case of all. The adults have a long seasonal range, occurring on the wing apparently throughout the year, and are apparently as numerous, if not more numerous, during the dry season. Since the larvae of some, if not all, may live in temporary as well

Notes on the Genus Erythemis

as permanent ponds, and since during the dry season the imagoes are numerous, it is very probable that the larval life is brief, and it is not improbable that the dry season is bridged by imagoes rather than by drought resistant eggs or larvae. We know that old and worn females, which might well have lived throughout the dry period, are still able to oviposit; and we know that when dry depressions become pools with the coming of the rainy season ovipositing individuals of species of several genera, including Erythemis, immediately put in an appearance.

It is not improbable that species of dragonflies whose larval life is spent in temporary pools and whose imaginal life is continued during the dry season are less bound to the vicinity of the location of these pools than are species whose larval life is spent in permanent bodies of water and which would therefore develop a stronger fixed habitat tendency through numberless generations of larvae and adults attached to a particular habitat. A longer larval life might also strengthen this tendency. It may be safely concluded that dragonflies emerging from temporary pools after a short larval life and with a long imaginal life, under favorable conditions for extended flight (the dry season in the tropics) before them, will be wide wanderers, and, other conditions permitting, species of wide distribution.

So far as species of Ervthemis are concerned, temperature is not a limiting factor over the large area included in tropical America. Swamps, ponds. pools, and lakes of varied characters, permanent and temporary, are abundant and widely scattered over this region, forming, with the exception of the southwest coast of South America, a practically continuous habitat. Species of Erythemis as imagoes are active and conspicuous, apparently living happy, care-free lives so far as predaceous enemies are concerned. They are voracious feeders on a varied diet of other insects, including species which are not dependent on bodies of water during their own lives, such as Lepidoptera. Hence, they can find a living anywhere and are not held to the immediate vicinity of their birthplace, as are many species whose imaginal food consists largely, if not entirely, of aquatic insects, and whose adaptability to a varied diet may be limited. Because of their larval life in both temporary and permanent pools, individuals are numerous as compared with other similar species whose larval life is confined to permanent pools, and, at the time of ovipositing, when active competition takes place, the males of one species protecting their own females against attacks and at the same time hustling away from the water the females of other species, Erythemis, because of its numbers and activity, is at no disadvantage. The eggs of Erythemis are dashed in the water and oviposition is as safe against parasitism of the eggs as it is in the other large number of species of similar habit. There is no reason to think the larvae of Erythemis are exposed to any particular danger. Their use of temporary pools would relieve them of competition or attack of many forms of aquatic life, while their successful use of permanent pools indicates they can meet the conditions there.

From the above considerations, we can understand the wide distribution of species of Erythemis which have been able to cross the great river valleys of South America, which valleys, marking frequently the broad areas which

separated earlier distinct continental land masses, have proved efficient barriers for many species. These valleys may be mechanical barriers or they may merely mark separate regions in each of which, through long adjustment, conditions have resulted which prevent the occupation of one region by many species from another region. Barriers, in any case, exist only in connection with specialized habits of dragonflies. For a high stream species a long mountain range might offer a continuous highway, which would be an insurmountable barrier for a low pond species. A long, broad valley, forming a great stretch of suitable habitat for the pond species, might prove an impassable barrier for the high stream species. In either case, if the river valleys are barriers, Erythemis has occupied and passed them, and if the higher regions themselves are exclusive to species from other regions, Erythemis, because of certain characteristics discussed and doubtless others, has successfully forced its way, at least to some extent, into the new environment. As a result, the present distribution of species offers, I believe, an unsolvable problem for the student who would determine the place of origin and trace the routes of distribution of the species of this genus. For example, Fundación, Colombia, lies in the relatively isolated Santa Marta region, and at this one station five species of Erythemis occur, and these five occur in Central America, the West Indies, and to the south to Paraguay. At Tucacas, Venezuela, four species have been recorded, and I have no doubt more careful collecting there would add at least two species. At El Banco, in the lower Magdalena, six species have been taken.

When we speak of the distribution of dragonflies or anything else, we imply, of course, the known distribution. The relation of the known distribution to the real distribution depends on the thoroughness with which collections are made. And this thoroughness depends on the number and distribution of collectors and the degree of success of each collector in obtaining everything in his specialty in each locality he works. And the collector's degree of success, other things being equal, depends on the relative conspicuousness of the things he collects. The imagoes of species of Erythemis are conspicuous insects, and the records of their capture are correspondingly Though collectors and localities visited in the past have been numerous. few in numbers with what we may expect in the future, probably our knowledge of the distribution of species of Erythemis corresponds at least in a broad way with the real distribution of these insects. Compare the status of our knowldge in this genus with that of some of the gomphines. for example. To cite one case, we know that the genus Erpetogomphus occurs in South America because of the capture, which might be described as accidental, of two specimens in Colombia and three in Venezuela-a total of five specimens for the continent.

DEFINITION OF THE GENUS

The following definition of Erythemis is compiled almost entirely from other authors. *Head* moderate or small; eyes joined for only a short distance; frons moderately prominent, rounded, without anterior ridge; vertex moderately high, apex slightly emarginate. *Hind lobe of prothorax* erect, as wide or wider than the other lobes, slightly or scarcely indentate in the middle posteriorly, the posterior and lateral margins with long hairs. Thorax moderately robust. Abdomen variable, stout to slender, inflated or not at the base, never distinctly dilated apically, segments 2 and 3, but not 4, each with a distinct median transverse carina. Legs stout, third femur of the male with an antero-ventral row of 15-30 small, regular teeth, and a postero-ventral row of similar but less numerous teeth, which rows reach from the base to about two-thirds the length of the femur, the apical third with three stout equal spines in the antero-ventral row and two of the same size in the postero-ventral row; second femur similarly formed with the basal rows of teeth shorter, reaching only about half the length of the femur. the number of teeth reduced and the apical spines variable in number, three or four in each row; third femur of female similar to second femur of male, ten or fewer teeth in the basal rows which reach from the base to, or not as far as, the middle of the femur, each row followed by 3 or 4 spines of unequal size; second femur of female similar to the third, but the apical spines reduced in number; spines on third tibia in both sexes stout, about 8 in each row, slightly weaker and less numerous on the other tibiae: claws of tarsi toothed before the tip. Accessory genitalia of male small, hamule two-branched. Abdominal appendages of male simple, superiors slightly constricted postbasally, then enlarging to beyond mid-length and then more rapidly reduced to a superior acute apex, a ventral row of small black teeth; inferior appendage triangular, shorter than the superiors, apex blunt or truncate, not deeply emarginate. Lateral margins of segments 8 of female not expanded. Vulvar lamina a more or less erect plate or trough. Wings long, moderately broad, the triangles at about the same level in front and hind wings, triangle of front wing narrow, the anterior side much shorter than the proximal, once crossed, triangle of hind wing and supertriangle of both wings free, subtriangle of front wing three-celled, sectors of arculus joined in a long stalk, arculus between first and second antenodal, base of triangle of hind wing at the arculus, 11-15 antenodals in the front wing, the last not continuous, one bridge cross-vein, one cubito-anal cross-vein in each wing, normally two cross-veins under the stigma, space between the last postnodal and stigma normal, not distinctly longer than adjacent spaces between postnodals, basal and apical parts of stigma about the same color, not distinctly bicolored, Cu1 and Cu2 in hind wing separate at origin, Rs and Rspl separated by one row of cells, M₂ with a single slight curve, not distinctly waved, Cu₁ in front wing strongly curved, the area between it and M₄ near their terminations in the wing margin wide, in front wing two (rarely three for one row's length) rows of cells between A and the hind margin of wing at level of arculus, anal field of hind wing broad, usually three (sometimes four and always two in credula) rows of cells between A₃ (A₂ of Laidlaw) and hind margin at level of base of triangle, two postanal cells in front wing, A, (Cuspl of Laidlaw) in hind wing slightly angled, the angle at about the level of distal angle of triangle, less rather than more distal, in hind wing three to five cells between Cu1 and Cu2 from triangle to distal angle of anal loop, one cell only between posterior angle of triangle and A2 (Cuspl of

Laidlaw) in hind wing, triangle of front wing followed by three cells (rarely two in credula) followed by three rows (usually but not always by two rows in part of the field in credula), increasing to more at or distal to the level of the distal cell between M4 and Mspl, hind wing with two postriangular rows of cells increasing to three at or distal to the level of forking of M_{1-2} and M_3 .

The striking difference in the form of the abdomen of haematogastra or plebeja, for example, on one hand and mithroides or peruviana on the other, more than any other one character, led authors, prior to Calvert in 1906, to distribute the species of Erythemis in three genera. But between the extremes named above the remaining five species may be arranged from more slender to less slender in approximately the following order: carmelita, credula, simplicicollis, attala, and collocata.

Another striking difference within the genus is the color of adults, especially of males, some having more or less of the body, but especially the abdomen, brilliant red, while in others no red or reddish appears in the coloration. This latter group includes some which are largely greenish or yellowish as tenerals and become dark bluish pruinose with age, while other darker species become deep black with age. This not-red group includes both slender and stout species, and also among the reds we have the extreme forms of abdomen. In the same way, among tenerals there are species with a distinctly patterned thorax and species which lack a definite pattern, the thorax being practically concolorous. And in each group are slender and stout species, and red and not-red species.

Thus, the species within the genus are well marked and easily recognized, but efforts to define more than one generic group seem futile.

In addition to the characters mentioned above, the accessory genitalia of the male and the vulvar lamina of the female are specifically distinct. In the case of the males, however, those individuals in which the penis is extruded usually, but not invariably, have the internal branch of the hamule bent outward and backward, so that the normal relation between the internal and external branches is lost.

KEY TO THE SPECIES OF ERYTHEMIS

Lateral and ventral carinas on abdominal segment 3 at the apex, measured along the apical carina, separated by .8 mm. or less; the distance between the same carinas, opposite the meeting point of the lateral and median transverse carinas, equal to more than one and one-half times the distance between them at apex; lateral and ventral carinas on segment 4 separated by a distance less than one-sixth the length of the lateral carina of segment 4 (possibly not always true of credula). Ventral teeth on the superior appendages of the male extending posteriorly beyond the level of the apex of the inferior appendage 2.

Lateral and ventral carinas on abdominal segment 3 at the apex, measured along the apical carina, separated by I mm. or more; the distance between the same carinas, opposite the meeting point of the lateral and median transverse carinas, equal to one and one-half times or less the distance between them at apex; lateral and ventral carinas on segment 4 separated by a distance greater than one-sixth the length of the lateral carina of segment 4 (possibly not always true of simplicicollis). Legs of adults largely black or dark brown......5.

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NOTES ON THE GENUS ERYTHEMIS

- 2 (1). Abdomen less than 30 mm. long, shorter than the hind wings. Dorsum of thorax distinctly patterned, paler above, bordered on either side with ante-humeral black or the thorax black. Yellowish or greenish to black insects. Male with the external branch of the hamule triangular in shape, the postero-ventral edge longer than the distance between the apex of the internal branch and the antero-ventral angle of the external branch. Female lamina short (not seen by me).....credula.

- 4 (3). Dorsum of abdominal segments 5-10 predominantly dark or black; dorsum of thorax distinctly patterned, paler above, bordered on either side with a black antehumeral band, or the thorax black. Yellowish or greenish to black insects. Male with external branch of the hamule directed ventrad, in posterior view erect. Female lamina from base of basal lobe to apex 1.5 mm.; apex of sternum of segment 9 with a patch of sparse bristles (80%) or with a single transverse row (20%)......plebeja.

- 5'. Labrum, face and frons not as above. Base of hind wings distinctly dark or at least (some females) tinged with yellow. Thorax yellowish or greenish yellow to red or black. Male with ventral teeth on the superior appendages extending posteriorly to about the same level as the apex of the inferior appen-

- 6 (5). Lateral and ventral carinas on segment 4 separated by a distance about onefifth the length of the lateral carina.....simplicicollis.
- 6'. Lateral and ventral carinas on segment 4 separated by a distance about onethird the length of the lateral carina.....collocata.

- 8(7'). Thorax largely dark or black, intricately patterned with paler, to completely black in old males. Abdomen black in old males, in others largely dark with conspicuous large basal or subbasal pale (yellow) areas, only narrowly separated by black in the median line, on segments 4 and 7. Dark colored to black insects. Lateral and ventral carinas on segment 4 separated by a distance equal to or less than one-fourth the length of the lateral carina. Male with the apex of the inferior appendage reaching beyond the level of the ventral teeth on the superior appendage. Female lamina in antero-ventral view nearly as long as wide, rounded triangular, slightly swollen at base on either side......attala.
- 8'. Thorax pale yellowish or greenish to dark red, without dark markings. Abdomen largely pale, yellowish to bright red. Pale colored to red insects. Lateral and ventral carinas on segment 4 separated by a distance equal to between one-third and one-fourth the length of the lateral carina. Male with the ventral teeth on the superior appendages extending posteriorly to about the same level as the apex of the inferior appendage. Female lamina in antero-ventral view trilobed, the width about one-half greater than the length....mithroides.

Erythemis carmelita, new species Plate I, figs. 1-6

Abdomen, male 31-31.5, female 32-33; hind wing, male 34.5-35, female 35; stigma, male 3-3.2, female 3.4-3.6.

Male.—Rear of head brownish red or yellow, labium yellow, darkening to red anteriorly and mesially, labrum orange, clypeus, frons, vesicle and occiput red, the last and the anteclypeus duller.

Prothorax and thorax yellowish or greenish red, possibly bright red in life in old males, unmarked. Legs yellowish (ochraceous-tawny of Ridgway), the antero-dorsal surface of the first femur and tibia black; second femur with the same surface largely black, and a narrow line of black on the same surface of the second tibia; third femur with the same surface with an ill-defined, restricted, subapical black area equal in length to about one-fourth the length of the femur; a narrow interrupted line on the same face of the third tibia; all tarsi darker, obscure to black; all spines and teeth on the legs, black, of usual form. Front wings at base with a trace of yellowish red. Hind wings with a yellowish red basal spot which anteriorly reaches the first antenodal and posteriorly is slightly more extensive, a few of the included cells sometimes with a dark reddish brown spot at the center. Stigma brown, narrowly shaded darker along the anterior edge.

Abdomen, including accessory genitalia and apical appendages red, the genitalia and appendages paler, yellowish; all unmarked, except for restricted black edgings on some carinas, especially on the apical carina; segments 4-9 in dorsal view shading apically into darker red. Abdomen inflated at base, 3 at base 5 high, 4, 1.6 high; 4-6 in dorsal view measure about as follows: 4, 1.6 wide at mid-length, and 4.8 long; 5, 1.9 wide and 4.6 long; 6, 2.1 wide and 4.4 long; 7-9 are about as wide as 6, 9 slightly narrower, and 10 is about 1.8 wide; in length, 7-10 are, respectively, 3.6, 2.4, 2, and 1. In profile at mid-length, 4 is about 1.1 high; from this point the abdomen gradually thickens posteriorly to the apex of 8, which is about 1.8 high. Lateral and ventral carinas on segment 3 separated at the apex by about .8, at the level of the point where the lateral meets the median transverse by about 1.6; on 4 the lateral carina is about 4.7 long and the lateral and ventral carinas are separated by a distance of .5 to .7.

Female.—Rear of head pale dull yellowish, a reddish brown spot on either side above and below against the eye, head pale as in the male but dull pale greenish brown without trace of red, the labium and anteclypeus yellowish.

Thorax dull green (about Saccardo's olive of Ridgway in dried specimens), unmarked. Legs slightly duller than in the male, similarly marked. Wings hyaline without basal markings or with yellowish red at the base to a varying extent, from a mere trace to, at the other extreme, in the front wings about one-third the distance to the first antenodal and in the hind wings slightly beyond the first antenodal. Stigma brown, narrowly shaded darker along the anterior edge.

Abdomen dull green, about the same color as the thorax, with 4-10 apically dark; 1-3 with the carinas slightly darker or more yellowish than the body of the segments; 4-7 shading to black apically, the apical third to half of each segment dark; 8-10 largely or entirely dark to black; the appendages and the lamina supra-analis lying between them yellowish to black, the latter about .67 long and I wide at base, triangular, the apex truncated, about .3 wide, and each posterior angle a rounded knob or tubercle so the apex is broadly emarginate or divided. Abdomen inflated at base, 3 at base about 4.5 high, 4 about 2.1 high; 4-6 in dorsal view measure about as follows: 4, 1.7 wide at mid-length and 5.6 long; 5, 1.9-2 wide and 5-5.2 long; 6, 2.1-2.4 wide and 4.8-5 long; 7-9 are about as wide as 6, 9 slightly narrower, and 10 is about 1.6 wide; in length, 7-10 are, respectively, 3.8-4, 2-2.4, 1.6-1.9, and .8-.9. In profile, at mid-length 4 is about 1.8 high; from this point posteriorly the abdomen is about the same height to near the apex of 8, the apex of which segment is 2.6-2.8 high. Lateral and ventral carinas on segment 3 separated at the apex by about .8, at the level of the point where the lateral meets the median transverse by about 1.2-1.4; on 4 the lateral carina is about 5.2 long and the lateral and ventral carinas are separated by a distance of .6-.7.

Venation, male and female.—Antenodals, front wing 13-15 (15 in 14%, 13 in 21%, 14 in 64%), hind wing 9-11 (11 in 14%, 9 in 28%, 10 in 57%); postnodals, front wing 9-10 (10 in 35%, 9 in 64%), hind wing 10-11 (11 in 14%, 10 in 85%). In front wing usually two rows of cells between A and the hind margin at level of arculus, but in four male wings the distal row of cells (the row against the subtriangle and the postanal cells) consists of three. In the hind margin. In hind wing 4+ cells between A_3 (A_2 of Laidlaw) and the hind margin. In hind wing 4+ cells between Cu_1 and Cu_2 from triangle to distal angle of anal loop, except in one female wing, where there are 5 cells. In anal loop 9-11 cells between A_2 and A_3 (Cuspl and A_2 of Laidlaw) (11 in one female wing, 9 in three male wings, 10 in all others).

Described from four males and one female, El Banco, Colombia, January 23-25, 1917; one male, Rio Neuvo, between Magangué and El Banco, Colombia, January 22, 1917 (both localities in the lower Magdalena River Valley); one female, Tucacas, Venezuela, March 23, 1920 (all above material in coll. E. B. W.); and one female, Boa Vista do Jaquiri, near the mouth of the Rio Teffé, Brazil, September 5, 1920, W. T. M. Forbes, coll. Cornell University. Type, the male from Rio Neuvo, allotype female, El Banco, January 25, 1917. Named in honor of Mrs. M. A. Carriker, Jr. (née Carmelita Flye), whose courage and industry as a member of Mr. Carriker's expeditions in the American tropics merit recognition.

Specimens of this species have been sent to Drs. Calvert and Ris, and both pronounce it new. Unfortunately, our notes give no particular data as to habits of the species. The male at Rio Neuvo was taken in a bit of dry (at that season) pastured woods. At El Banco we collected a variety of habitats, but most of our material was taken in dry (at that season) woods and brush adjoining the river, and nearly dried up adjacent pools. At Tucacas on March 23 we collected at a large lagoon, possibly an old river bed, lying on the north side of the railroad and between four and five kilometers out of town. This lagoon has large areas of deep open water bordered at places by more extensive low areas filled with rosette-leaved plants, sedges, grasses, and several species of bushes. At places large areas of this sedgy, brushy marsh were floating on the deeper waters of the lagoon, and about such places, crocodiles were very numerous. The more solid ground about the lagoon is covered with pastured grass, dense thickets of small spiny trees or shrubs, and forests. Strong flying libellulines are numerous about the margins of the deeper water in the lagoon.

NOTES ON THE GENUS ERYTHEMIS

Carmelita is separated from all other species by its paler legs. It is separated from the less densely veined, very distinct and smaller *credula* by venational characters indicated in the definition of the genus. With the exception of *simplicicollis* and *collocata*, the species of Erythemis are very distinct and it is difficult to distinguish relationships within the genus. However, *carmelita* is probably more closely related to *haematogastra* than to any other species. Characters given in the key readily separate them.

A List of the Species Recorded in this Paper, with Places and Dates of Capture¹

The species are arranged alphabetically and numbered consecutively. Following each locality under each species are numbers in parentheses indicating the other species taken at the same place. For example, *E. plebeja* Burmeister. *Venezuela:* Encontrados, (1, 5, 6), indicates that *attala, mithroides*, and *peruviana*, in addition to *plebeja*, were taken at Encontrados.

1.	Erythemis	attala Selys	5.	Erythemis	mithroides Brauer
2.	"	carmelita Williamson	6.	"	peruviana Rambur
3.	**	credula Hagen	7.	"	plebeja Burmeister
4.	""	haematogastra Burmeister			

1. Erythemis attala Selys. Colombia: Fundación, (4, 5, 6, 7), January 13, 1917; El Banco, (2, 4, 5, 6, 7), January 23 and 25, 1917. Venezuela: Palma Sola, (5, 6, 7), March 8, 1920; Encontrados, (5, 6, 7), April 25, 1920.

Attala is a widely distributed and therefore apparently a common species, but I have never found it in great numbers at any particular habitat. In fact, the total Colombia-Venezuela catch numbers only four males and three females. However, Bates, as recorded by Ris, notes: "Dry woods at Santarem, very common, much more abundant than *plebeja*." As opposed to my general statement that tropical species of the genus are probably on the wing throughout the year is the fact that Hine and I failed to get attala at Amatillan, Gualan, and Los Amates, in Guatemala, in January, 1905, while I took it at the three localities in June, 1909. But available records show attala on the wing somewhere every month in the year, except September, November, and December, and there is no doubt it flies these months, too; and our failure to find it in January in Guatemala was probably due to its relative scarcity and to its having deserted the permanent bodies of water (where we did most of our collecting) to range about in the dry brush.

¹ For notes on localities, see: A Collecting Trip to Colombia, South America, by E. B. Williamson, *Miscellaneous Publications, Univ. of Mich., Mus. of Zool.*, No. 3, February 22, 1918; and Notes on the Habitats of Some Tropical Species of Hetaerina, by E. B. Williamson, *Occ. Papers, Univ. of Mich., Mus. of Zool.*, No. 130.

Localities not discussed in these papers or in the description of *E. carmelita* are briefly described at the end of this paper. The student may be interested to note that at the following locations, described in *Occasional Papers*, No. 130, no species of Erythemis have been recorded: Aroa, Boqueron, Cincinnati, Cristalina, La Fria, Maraquita, Nirgua, San Esteban, and Tachira.

The elevation of the three Guatemalan localities mentioned are, moreover, above the apparently optimum habitats of species of Erythemis (due probably rather to the relative absence of such pools as occur at lower levels than to elevation itself), and it may be noted that on February 5, 1905, we found the species at sea level at San José, Guatemala.

Attala is an active species in a genus of generally active species, and at times individuals are seen whose incessant activity and wariness effectually prevent their capture. It is a matter of common observation among strongflying species of dragonflies that in an assemblage of only a few individuals of a species such individuals are much more wary of the collector than individuals in a numerous assemblage when their attention is largely given to each other, and the collector finds their capture less difficult. This will often explain the extreme wariness of *attala* which, as stated above, has not been noted as very numerous about any particular habitat in Colombia or Venezuela.

2. Erythemis carmelita Williamson. Colombia: Rio Neuvo, (5, 6), January 22, 1917; El Banco, (1, 4, 5, 6, 7), January 23-25, 1917. Venezuela: Tucacas, (5, 6, 7), March 23, 1920. See description of this species in this paper for further notes.

3. Erythemis credula Hagen. Panama: Gamboa, Canal Zone, (6), August 5, 1920, J. H. Williamson.

Credula is apparently, next to *carmelita*, the rarest species of the genus and J. H. W.'s record for Panama is the first for Central America. I have seen the species alive at only one locality, Pitch Lake, Trinidad, where the males were flying about the small pools of water in the pitch.

4. Erythemis haematogastra Burmeister. Colombia: Rio Frio, (5, 6, 7), January 8, 1917; Sevilla, December 15, 1916; Fundación, (1, 5, 6, 7), January 12 and 13, 1917; El Banco, (1, 2, 5, 6, 7), January 24 and 25, 1917; Puerto Berrio, (5, 6), January 8 and February 21, 1917. Venezuela: El Guayabo, (5, 6, 7), April 20, 1920.

Bates, as recorded by Ris, notes: "Rather common species at Santarem; it frequents only the shade of the woods and settles frequently on dried twigs. Banks of brooks, Pará, not uncommon." So far as I have observed, this species is rare, being found usually only as a solitary individual sunning itself on some twig or broad leaf near or far from water. In fact, the total Colombian-Venezuelan catch numbers only fifteen specimens, nine males and six females; the number of specimens taken at each locality varies from one to three, except at El Banco, where five specimens were collected.

5. Erythemis mithroides Brauer. Colombia: Santa Marta, (7), December 19, 1916; Rio Frio, (4, 6, 7), January 7, 1917; Fundación, (1, 4, 6, 7), January 13 and 14, 1917; Bolivar, (6, 7), December 20, 23, and 26, 1916; Rio Neuvo, (2, 6), January 22, 1917; El Banco, (1, 2, 4, 6, 7), January 23-25, 1917; Puerto Berrio, (4-6), January 30, 1917. Venezuela: Tucacas,

(2, 6, 7), March 23 and 24, 1920; Palma Sola, (1, 6, 7), March 4, 6, and 10, 1920; Encontrados, (1, 6, 7), April 23 and 25, 1920; El Guayabo, (4, 6, 7), April 20 and 22, 1920.

In life *mithroides* is a rich-colored and active species, usually with lower flight than the slender species *haematogastra* and *plebeja*, which are possibly more wary and active than *mithroides*. About the ponds where *mithroides* often occurs in considerable numbers it is often seen resting on the leaves of coarse grasses and sedges, its color and activity making it conspicuous. We have found it in numbers on several occasions: the pond on the upper side of the railroad out from Santa Marta and just beyond the bridge over the Manzanares; the large swamp south of Mamatoca near Bolivar; and the little ponds along the railroad and beyond the Caña Fraile out from El Guayabo.

One of two males taken at Rio Neuvo has the triangle of both front wings free. One of the large males taken in Guatemala and described by Dr. Ris (Coll. Selys, p. 1173) was referred to Dr. Kennedy, who kindly examined the penis of the specimen and found it agreeing with penes of smaller specimens of the species.

6. Erythemis peruviana Rambur. Panama: Gamboa, Canal Zone, (3), August 5, 1920, J. H. Williamson. Colombia: Rio Frio, (4, 5, 7), January 4 and 6-8, 1917; Fundación, (1, 4, 5, 7), January 10 and 12, 1917; Bolivar, (5, 7), December 19, 23, and 26, 1916; Rio Neuvo, (2, 5), January 22, 1917; Magangué, January 21, 1917; El Banco, (1, 2, 4, 5, 7), January 24, 1917; Las Delicias, January 28, 1917; Puerto Berrio, (4, 5), January 31 and February 8, 1917. Venezuela: Tucacas, (2, 5, 7), March 23 and 24, 1920; Palma Sola, (1, 5, 7), March 4, 6, 8, and 9, 1920; Bejuma, (7), February 16, 1920; Encontrados, (1, 5, 7), April 23, 25, and 26, 1920; El Guayabo, (4, 5, 7), April 20, 1920.

Bates, as recorded by Ris, states: "Banks of brooks near Pará, Obydos very plentiful." In fact, this species may occur about some favored habitat in possibly larger numbers than we have ever seen any other species of the suborder Anisoptera. Under such circumstances, usually about a pond or muddy, sluggish, and sun-exposed creek or ditch, most, if not all, of the individuals will be teneral or lacking the colors of the fully adult. However, a few mature ones in full flight, by their restless activity and general impertinence toward other species, may make collecting of other Anisoptera at the same habitat difficult or well-nigh impossible. And when at some swamp or pond the collector finds *peruviana* represented by only one or two adult males, he will usually find the capture of these a difficult or even impossible feat if he depends solely on his insect net.

As in other species observed, the females of *peruviana* are more voracious feeders than the males. A female taken at Encontrados, Venezuela, was feeding on a butterfly, *Thymelicus athenion* Huebner, as determined by Mr. William Schaus. In fact, Lepidoptera seem to be a favorite food for species of Erythemis, and I have records of *simplicicollis* in Indiana feeding on *Thecla liparops* Bd. and Lec., and *Haploa confusa* Lyman, both determinations by Dr. Dyar.

In marked contrast to the dull, common-looking tenerals and females, the fully adult males of *peruviana* are among the most brilliant and handsome of dragonflies. In flight they are swift and agile, and suggest *simplicicallis*, but I have never observed them indulging in the complicated evolutions of the latter species.

7. Erythemis plebeja Burmeister. Colombia: Puerto Colombia, December 10 and 11, 1916; Santa Marta, (5), December 13, 16, and 18, 1916, and January 3, 1917; Don Jaca, December 17, 1916; Rio Frio, (4, 5, 6), January 4-8, 1917; Fundación, (1, 4, 5, 6), January 13, 1917; Bolivar, (5, 6), December 20, 21, 23, and 26, 1916, and January 2, 1917; Zambrano, January 20, 1917; El Banco, (1, 2, 4, 5, 6), January 23, 1917; Gamarra, January 27, 1917. Venesuela: Tucacas, (2, 5, 6), March 23, 25, 1920; Palma Sola, (1, 5, 6), March 8 and 10, 1920; Bejuma, (6), February 13, 18, and 24, 1920; Encontrados, (1, 5, 6), April 25, 1920; El Guayabo, (4, 5, 6), April 20, 1920.

A male of this species, collected in Jamaica and received from Carpenter, is labelled *haematogastra*, but I do not think this mistake is likely to be frequent as, if any confusion occurs as regards *plebeja*, it is likely to be with *attala*; and as Calvert has pointed out, the adult male of *haematogastra* superficially resembles the adult male, not of another Erythemis, but a species of another genus, *Rhodopygia hollandi*, just as another Erythemis, *peruviana*, superficially resembles *Planiplax sanguiniventris* rather than some other species of Erythemis.

Bates, as recorded by Ris, states of *plebeja*: "Banks of the river Tapajos near Santarem, settling on bushes in the woods." It is an agile species and is found widely scattered in practically all the environments of any locality where it occurs.

CONCLUSIONS

Finally, I should like to call attention to the present status of Erythemis and a very different genus of American dragonflies, Hetaerina, and to certain facts in their life histories, leaving to other students any conclusions as to the significance of these facts in explaining present conditions. There are nine known species of Erythemis as against about fifty species of Hetaerina. And yet, in any locality (an area three to ten miles in diameter) the largest known list of Hetaerinas is four species, or eight per cent of the total, while in Erythemis the largest local list is six species, or sixty-six and two-thirds per cent of the total. Moreover, in any locality the species of Erythemis there tend to more fully occupy the various environments of the locality than do Hetaerinas, or one environment in the locality may harbor all the Erythemis found there, while these conditions are usually reversed in Hetaerinas, each species often showing a marked preference for a certain ecological habitat.

The species of Erythemis, as larvae, live in stagnant water, and Hetaerinas live in running water. Streams offer a greater variety of ecological conditions than fresh-water ponds offer.

Hetaerinas as imagoes are closely bound to the streams which make their larval home. Their dispersal to new habitats is doubtless rare and accidental.

NOTES ON THE GENUS ERYTHEMIS

It is entirely conceivable that a single fertile female in a certain instance might furnish the entire original Hetaerina invasion of the headwaters of some small mountain creek. Here the species, by direct descent from this single female, might maintain itself without any admixture of new blood for many generations. After a period of time, the infrequent and accidental invasion by new blood would be quickly swamped in the mass of old stock. Individuals of Erythemis, on the other hand, are wanderers, and the Erythemis fauna of any pond may be partly or largely descended from new immigrants of the preceding season, their descendents in turn scattering with the dry season and many of them visiting other ponds when the period of ovipositing comes.

Specimens of any species of Erythemis are remarkably uniform throughout the range of the species. I know of only one exception, that of the Guatemalan specimens of E. mithroides, which are distinctly larger than South American specimens of the same species. On the other hand, a number of cases of differences in a species of Hetaerina in its range can be cited. The most striking case I recall is the remarkably large, dark specimens of *cruentata* occurring at a high elevation in the isolated Santa Marta Mountains of Colombia. Almost equally striking is the large, dark form of *macropus* at an elevation of 2,230 feet in Peru. On a larger scale, but less distinctly marked, are the pale forms of *caja* and *macropus* east of the Andes in western Venezuela, as compared with the dark forms west of these mountains.

LOCALITIES NOT HERETOFORE DESCRIBED IN THIS OR OTHER PAPERS

1. Bejuma, Department of Caraboba, Venezuela. In describing the country about Bejuma in Occasional Papers, No. 130, several swamps or shallow ponds which lie in the valley were not mentioned. One of these is about one mile east of Bejuma. The area is about an acre, surrounded by thorny mimosas inside which grew several species of sedges, water hyacinth, another aquatic with three yellow petals, orange at the base, another with small purple flowers, and a small yellow Utricularia. This pond was in the last stages of drying up when we saw it on February 16, 1920, with very little open water, which had a maximum depth, with the mire in which one sank, of about three feet.

2. Encontrados, Department of Zulia, Venezuela. Encontrados is on the right bank of the Catatumbo River and is the lower terminus of the Gran. Ferrocarril del Tachira. Its elevation is about 138 feet, and it lies in a low, flat country of brushy forest, large areas of which near town and along the railroad are now in grass, bananas, cocoa, and some sugar cane. Just above town is a long lagoon filled with aquatics and bordered with brush and pastures where odonate life, especially strong-flying libellulines, was very abundant. Along the river below town are many flats, covered with water during the rainy season, and during the dry season consisting of stretches of mud, grass, and bushes, with shallow pools. Three or four kilometers below town on the left river bank is a caña eight to twelve feet wide, mostly in the sun,

muddy and with many logs, the banks high and grass-covered, and the adjacent country in corn, bananas, and abandoned fields, with occasional patches of forest with heavy brush and frequent dense Heliconia growths. These bits of forest are often bordered and sometimes completely surrounded by an impenetrable jungle of spiny shrubs overgrown with razor-edged sawgrass.

3. Las Delicias, Department of Magdalena, Colombia. A woodpile on the banks of the Magdalena about 120 leagues above Barranquilla and two or three leagues below Boca de Rosario. The surrounding country is the usual low, level-lying river plain of the lower Magdalena.

4. Zambrano, Colombia. A village on the Magdalena between Calamar and Magangué in the usual level, pastured land of the lower river valley.

THE PHYLOGENY AND THE GEOGRAPHICAL DISTRIBUTION OF THE GENUS ERYTHEMIS (ODONATA)

By CLARENCE HAMILTON KENNEDY

The following paper has been prepared at the suggestion of Mr. E. B. Williamson, who, in the accompanying paper, has presented the systematics of this group. The material has been arranged to parallel the arrangement in the writer's article¹ on the genus Libellula, and is one of a series of papers which it is planned to present on the relationships of the American Odonata.

Time is not available and material is not at hand for a definition of the relationships of this genus to the other genera in the Libellulinae. For this reason, the writer has followed the definition of groups presented by Ris,² who followed Calvert.3 The penes of Lepthemis and of all the species of Ervthemis recognized by these authors have been examined. Ris includes in this group only one other genus, Rhodothemis of the East Indies. As no material of this species is in Mr. Williamson's or the writer's collections, it has not been studied. However, Ris figures its wings and gives a detailed description of its peculiarities. From this account it is evidently the least specialized of the three genera in the armature of the legs, which have the spines of the femur less developed; and in the venation, which is "reduced" as it is in credula only of the American genera. The location of Rhodothemis, the least specialized member of this series, in the East Indies suggests an Oriental origin for the group as a whole and that the stock of the American genera at some time in the past has spread into its present habitat. As the majority of the species are tropical, the spreading into America may have taken place when the Asia-Alaska land-bridge had a climate suitable for such species, which must have been in Pre-Miocene times. The other possibility is that they came across from Africa, but so far we have not recognized any African relatives of the group. Credula, the most primitive of the American species, has not been found north of Panama and St. Thomas, while the two species that are found farthest north, haematogastra4 and simplicicollis, are two of the most specialized, which distribution seems to confirm a southern or tropical entrance into America.

The homologies of the lobes of the penis in the genera Libellula, Sympetrum, Orthetrum, and Orthemis were worked out by the writer in a previous article.⁵ All parts that were defined for these appear also in the series

⁵ The Morphology of the Penis in the Genus Libellula. Ent. News, XXXIII, pp. 33-40, 1921.

¹ The Phylogeny and the Geographical Distribution of the Genus Libellula (Odonata). Ent. News, XXXIII, pp. 65-71, 105-111, 1922. 2 "Libellulinen," Fasc. XIII, pp. 591-608 in Coll's Zool. du Selys, 1911.

³ Nomenclature of Certain North American Odonata, Ent. News, XVII, pp. 30-31, 1906.

⁴ Williamson doubts the Georgia records of this species.

of Erythemis penes. In comparison with the penes discussed in the above article, the first peculiarity in the Erythemis penes that strikes one is the development of a small, chitinized, two-lobed hood over the medial lobes. Apparently, it is a specialization of Erythemis and its near relatives. It appears in all the species except *credula*, in which species the penis is most like that organ in the less specialized members of Libellula, Sympetrum, etc. As this species has the generalized characters of venation found in Rhodo-themis, we have considered it the most primitive of the American species of the Erythemis series. Even though it lacks this hood, there is no doubt that *credula* belongs in or next to Erythemis, as it has in a pair of tubercles the homologue of the hood in the other species (see fig. 8).

The American species, by penis characters, divide into four groups which are exactly equivalent with the groups as outlined by Calvert and Ris on other characters. To these, Rhodothemis rufa may be added as an extra group. In the key I have placed it first as Group I because of its generalized characters. The fifth and largest group is composed of species with penes so much alike that no good characters appear on which to divide them further, though they seem to fall into two sub-groups on the shape of the abdomen. The writer would be inclined to call the whole series of five or six groups Lepthemis and would consider the individual groups as subgenera, which could be given generic rank by those who wish to use smaller genera. Lepthemis, for the whole series from Rhodothemis rufa to Erythemis haematogastra, is no more comprehensive, in the writer's opinion, than Libellula for the series of species included in the latter by Ris and later by the writer. The comprehensive genus would have to be Lepthemis because of the priority in the use of that name by Hagen.⁶ The groups may be outlined as follows:

I.	Oriental (Rhodothemis)Group I-rufa			
ı' .	American (Lepthemis and Erythemis) 2.			
2 (1').	Hood over medial lobes undeveloped (represented by two tubercles)Group II-credula			
2'.	Hood over medial lobes developed into an arched two-lobed affair 3.			
3 (2').	Posterior lobe of penis lacking, the three cornua fused into a single conspicu- ous, terminal lobe			
3'.	Posterior lobe present 5.			
4 (3). Lateral lobes and cornual lobe parallel to the axis of the penis (Lepthemis) Group III—vesiculosa				
4′∙	Lateral lobes and cornual lobe bent across the axis of the penis (Mesothemis)			
5 (3').	Abdomen not especially slender (Erythemis) Group VA—peruviana mithroides attala			
5(.	Abdomen slender (Erythemis)GroupV B-plebeja carmelita haematogastra			
⁶ Synopsis of the Neuroptera of North America, p. 160, 1861.				

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This series of eleven species, small as it is and with several of its species occupying nearly identical habitats, is so non-committal as to its origin and routes of migration that these will have to be worked out by some less direct method than that of a study of the degrees of specialization of the individual species. The latter method gives results where the group is large and many connecting links remain.

It is possible that *vesiculosa* belongs near Group V B and that the loss of the posterior lobe has occurred independently in Groups III and IV. A careful check of the other characters should decide this.

We have also the problems of the generic rank of Mesothemis and the value of its two forms, *collocata* and *simplicicollis*. By penis characters alone, Mesothemis is as valid a genus as Lepthemis. In fact, the specialization of the fusion of the lobes of the cornua and the loss of the posterior lobe has gone farther from the Erythemis type that is found in the majority of the Erythemis species than it has gone in the Lepthemis penis. The forms, *collocata* and *simplicicollis*, as viewed in the light of recent work by geneticists on other insects, are probably good species. Just how nearly homozygous each is under all circumstances will have to wait until a careful study can be made of the two forms where their habitats overlap.

EXPLANATION OF PLATE I

Figs. 1-6, by E. B. Williamson.

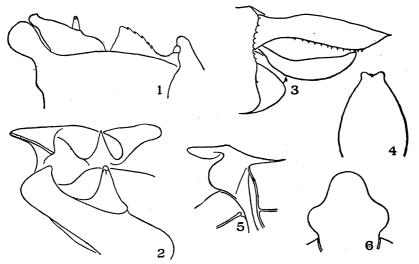
Figs. 7-16, by C. H. Kennedy.

Figs. 1-6, *Erythemis carmelita* n. sp. Figs. 1-4, type male; figs. 5-6, allotype female. Fig. 1, accessory genitalia of segment 2 in lateral view; fig. 2, same in latero-ventral view; fig. 3, abdominal appendages in lateral view; fig. 4, inferior appendage in ventral view; fig. 5, vulvar lamina in lateral view; fig. 6, the same in antero-ventral view.

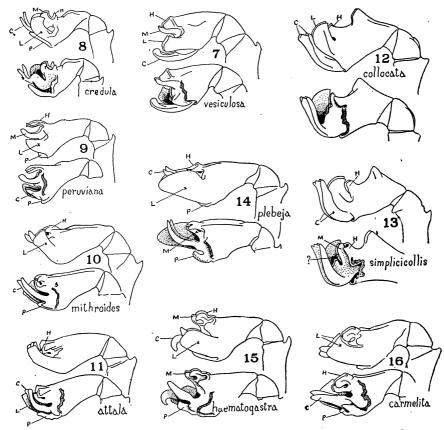
Figs. 7-16, penes of species of Lepthemis and Erythemis. Each pair of figures represents, in the upper member, a lateral view of the tip or third segment of the penis and, in the lower member, the same view with the lateral lobe removed to show the cornual and medial lobes. Where not otherwise indicated, the specimen is in the collection of Mr. E. B. Williamson. The lettering of the figures is that used in "The Morphology of the Penis in the Genus Libellula," Ent. News, XXXIII, pp. 33-40, as follows: H = hood, M = medial lobes, C = cornua, L = lateral lobes, P = posterior lobes.

Fig. 7, Lepthemis vesiculosa, Dutch Guiana, O. S. U. coll.; fig. 8, Erythemis credula, Pitch Lake, Trinidad; fig. 9, Erythemis peruviana, Tucacas, Falcon, Venezuela; fig. 10, Erythemis mithroides, El Banco, Colombia; fig. 11, Erythemis attala, Fundacion, Colombia; fig. 12, Erythemis collocata, Fresno Beach, California; fig. 13, Erythemis simplicicollis, Columbus, Ohio; fig. 14, Erythemis plebeja, Fundacion, Colombia; fig. 15, Erythemis haematogastra, Fundacion, Colombia; fig. 16, Erythemis carmelita, El Banco, Colombia.

LEPTHEMIS AND ERYTHEMIS



E. carmelita n. sp.; figs. 1-4, type male; figs. 5-6, allotype female.



Penes of the species of Lepthemis and Erythemis, figs. 7-16.

