REVIEW OF THE NEOTROPICAL DAMSELFLY FAMILY DICTERIADIDAE (NEW SPELLING), WITH AN ANNOTATED BIBLIOGRAPHY (ZYGOPTERA)

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A review of all names associated with the Dicteriadidae (corrected spelling for Dicteriastidae) shows that only 2 genera, each monotypic, are valid. A study of over 125 specimens revealed remarkable intraspecific variability in venational characters formerly considered stable and conservative. The valid species are Dicterias atrosanguinea Sel. and Heliocharis amazona Sel. Neocharis, Charitopteryx, and Cyanocharis are new synonyms of Heliocharis. Heliocharis braziliensis Hag., H. libera Sel., Cyanocharis valga Needham, and Neocharis cothurnata Foerster are new synonyms of Heliocharis amazona. Notes on biology and an annotated bibliography are included.

INTRODUCTION

A group of damselflies unique to South America and referred to in most recent literature as Dicteriastidae or Heliocharitidae has had an extraordinarily tangled taxonomic history in five languages. A total of 3 family names, 5 genus names, and 9 species names have been associated with the group. All of the species were described from only 1 to 3 specimens, with the descriptions based mostly on wing venation; no species was differentiated from another on the basis of body morphology, including genitalia. Unfortunately, the venation in this group is variable, even in conservative characters considered stable in other Odonata.

Specimens of this family are generally rare in collections, but are of considerable phylogenetic interest (FRASER, 1957). Based on a study of all literature on the group, and of over 125 specimens, I believe that only 2 valid species, each in a monotypic genus, have been described in this family. These are the first 2 species described in the group, *Dicterias atrosanguinea* and *Heliocharis amazona*, both

described by SELYS (1853). D. atrosanguinea is a small species whose male has a red abdomen, H. amazona is a large species with a predominantly blue male abdomen. The venation of the distal half of the wings is also very different in these genera. Thus it is difficult to understand how some of the species described later were placed in the wrong genera.

Specimens for this study were obtained from the people and institutions listed in the acknowledgements; I have enclosed one of my determination labels with each specimen examined (all specimens in cellophane envelopes).

DICTERIADIDAE

FAMILY NAME

This group of damselflies has been classified under many different family-level names. Most recently, when the group has been considered a separate family, these have been Heliocharitidae, introduced by TILLYARD & FRASER (1939), Dicteriastidae, first used by MONTGOMERY (1960), and Dicteriidae, introduced by RACENIS (1968). None of these authors explained the derivations of their names, although MONTGOMERY (1962) later briefly explained his reasoning. Which of the above names, if any, is correct? The Third Edition of the *International Code of Zoological Nomenclature* (1985), hereafter called the Code, stated in Article 35d(i) that "An incorrectly formed family group name... must be corrected".

The history of this group was begun by SELYS (1853, p. 6) in a chart, where he listed the "legion" Dicterias, containing the "genus" Heliocharis with its "subgenus" Heliocharis, and below those in the list, the "genus" Dicterias with its "subgenus" Dicterias. Selvs' use of the same word for different taxonomic levels has led to considerable confusion in later literature. As MONTGOMERY (1962) pointed out, Selys' "legions" correspond to a modern family-level group, his genera to a subfamily, his subgenera to modern genera. SELYS' (1853) chart already set the stage for controversy on the family name, because some authors have used Heliocharitidae after the first listed genus. Under the legion Dicterias, SELYS (1853) described both Heliocharis and Dicterias as subgenera on page 55, but Heliocharis first. Thus Heliocharis also became the first described genus in the family. However, Article 64 of the Code states: "An author who establishes a nominal family-group taxon may choose as type genus any included nominal genus the name of which he or she regards as valid... not necessarily that having the oldest name". SELYS (1853) obviously regarded Dicterias as the type genus for a family-group taxon, so Dicterias is the name on which the family name must be based, "Dicterias" is the Latin transliteration of the Greek "deikterias", meaning a female mime. Perhaps Selys had in mind that Dicterias was similar to or mimicked some other damselfly. Article 29b(i) of the Code states that the stem for a family name is found by deleting the case ending of the genitive singular, in this case "deikteriados", transliterated to Latin as "dicteriados". Thus, deleting the "-os" and adding "-idae", the family name becomes Dicteriadidae. According to Article 11f(ii) of the Code, Dicteriadidae is to be attributed to Selys, 1853.

SELYS (1854) hinted that a "d" suffix might be part of the name for a higher taxon when he listed "Genre VIII. — DICTERIADE (Dicterias, De Selys.)". Apparently Dicteriade corresponded to SELYS' (1853) genus (= subfamily) category, and has never been used again.

SELYS' (1853) one sentence description of the family referred only to venation. TILLYARD & FRASER (1939) more fully characterized the family, as Heliocharitidae, again entirely on venation, and FRASER (1957) repeated that description. DAVIES (1981) briefly characterized the family as Dicteriastidae, and DAVIES & TOBIN (1984) repeated that description.

RELATIONSHIPS

No fossils of Dicteriadidae are known. KENNEDY (1919) placed this group in his Agrioninae but noted that it connected the broadwinged Agrioninae with his Amphipteryginae. TILLYARD & FRASER (1939) and FRASER (1957) placed the Dicteriadidae between Polythoridae and Amphipterygidae. CARLE (1982a, 1982b) placed the Dicteriadidae between Polythoridae and Calopterygidae, with the dicteriadids separating from the polythorids about 100 million years ago. DE MARMELS (1989) considered Dicteriadidae closely related to Megapodagrionidae, based on larval and adult morphology, and adult behavior. These varied opinions are a reflection of the lack of a consensus on the higher classification of the Odonata.

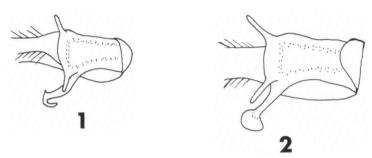
DICTERIAS ATROSANGUINEA SELYS, 1853 Figure 1

Dicterias procera Hagen in SELYS, 1859 — [Synonymized by HAGEN, 1875].

MORPHOLOGY AND VARIATION

The only extensive description of *D. atrosanguinea* is that of the holotype male by SELYS (1854). Ten males I examined (no females available), probably better preserved than the holotype, allow a more accurate description of coloration: Clypeus black, rest of face sky blue, labium and rear of head mostly pale yellow. Prothorax olivaceous marked with brown, pterothorax bluish yellow with black mid-dorsal stripe and metallic red-brown mesepisternal, mesepimeral, and metepisternal stripes; mesepisternal stripe wide, covering lateral 2/3 of mesepisternum. Coxae and undersurface of trochanters gray-yellow, remainder of legs dark

brown. Sides of abdominal tergites 1-2 gray-yellow, remainder of abdominal tergites bright red. Male gonapophyses pointed posteriorly as in *Heliocharis amazona*. Penis (Fig. 1) like that of *H. amazona* (Fig. 2; figs in KENNEDY, 1920), but each lateral lobe tipped with a recurved hook rather than a spatulate expansion.



Figs 1-2. Penes of Dicteriadidae: (1) *Dicterias atrosanguinea*, right lateroventral view (Brazil, Amazonas, 26 km E Manaus); — (2) *Heliocharis amazona*, same view and scale (Brazil, Rodonia, 60 km S Ariquemes).

SELYS' (1854) measurements of the holotype were slightly larger than in my 10 males (mm): total length 39, abdomen 30, hindwing 23, compared with 34-37, 26-28, 21-22. The hindwing was 77-81% as long as the abdomen, within the range found for *H. amazona*. The venation of the present 10 males was similar to that of the holotype: no midbasal crossveins, 1 quadrangular crossvein (except 0 in 1 wing, 2 in 1 wing), 1 subcostal crossveins, 1 row of cells posterior to Cu2 (Needham notation), nodus at 36-38% length of hindwing, M1-2 bowed anteriorly to touch R (not quite touching in 9 wings of 5 males). Thus *D. atrosanguinea* is a smaller species with apparently less variable venation than *H. amazona*.

REMARKS ON TAXONOMY

SELYS (1853) described the genus, then characterized it more fully in 1854. SELYS (1853) described the species as "Dicterias atrosanguinea, Dale, MS". In all of his further writings (1854, 1869, 1873) SELYS continued to ascribe the name to Dale. Because the original description was apparently by Selys, and since Dale never published anything on the species, Selys is the describer. All other writers, beginning with HAGEN (1861), have given Selys as the author of the species. Apparently at least 3 males of D. atrosanguinea were known at the time of the original description because SELYS (1853) mentioned specimens from Para [Brazil] in the collections of Dale, Saunders, and Selys. The species was also listed from the British Museum by WALKER (1853). However, SELYS used only his own single male to write the description, because he stated in 1854

"inferior appendages not visible in the example which I possess". The holotype male is in the Selys Collection in Brussels, Belgium.

SELYS (1854) illustrated a wing, the mouthparts, and abdominal segments 9-10. MUNZ (1919) repeated Selys' wing drawing, and NEEDHAM (1933) gave drawings of both fore- and hindwings.

SELYS (1869) very briefly described the female, and noted that both females and young males were olivaceous.

The entire original "description" of Dicterias procera Hagen in Selys, 1859 reads: "Very analogous in form and coloration to D. atrosanguinea, but body larger. Native land: Santarem, in the Amazon, sent by M. Bates (British Museum)". Apparently Bates sent the specimen(s) directly to the British Museum and Selys wrote the above from information provided by Hagen. SELYS (1869) still had not seen a specimen, for he wrote: "It could be that D. procera... which I have not seen in nature [specimens] is identical with Heliocharis libera". This was total speculation because H. libera Selys is a synonym of the much different H. amazona Selys. SELYS (1873) listed both D. procera and H. libera as questionable races or synonyms of H. amazona. HAGEN (1861) listed "Dicterias procera Hagen!" as a species, indicating (by the!) that he had seen the type, but HAGEN (1875) finally synonymized it with D. atrosanguinea. The location of the type (male?) of D. procera, apparently originally in the British Museum, is not known (S. Brooks, pers. comm.).

NEEDHAM (1933) illustrated the wings of *Dicterias procera* but did not state why he chose that name or from where the specimen came. Needham wrote: "With the figure of the wing of *Rima*, we present a drawing of *Dicterias* (from the same region)...". RACENIS (1966) apparently took "the same region" to mean Mt Duida, Venezuela, the type locality of *Rima*, and listed *D. procera* from Venezuela on that basis. I suspect that NEEDHAM (1933) actually meant Amazonian Brazil, because *Dicterias* is not mentioned elsewhere in his 1933 paper. DE MARMELS (1990) deleted *Dicterias* from the Venezuela list.

BIOLOGY

Two features of adult Dicteriadidae attract particular attention: the long nearly bare legs, unique among the Odonata, and the large movable hook on each labial palp, the latter longer and sharper than in any other adult zygopteran with which I am familiar. I speculate that they use their legs less for capturing prey than do other Odonata, but use the large movable hooks to assist in aerial prey capture. The femora of the prothoracic legs of adult dicteriadids are curved so that they fit snugly against the mesepisternum when the leg is folded dorsally. During flight, this mechanism probably decreases air resistance resulting from the length of the legs.

The larva of D. atrosanguinea is unknown, and nothing has been recorded of

the adult's behavior.

No flight dates are given in the literature, and the only definite literature distributional record is Santarem, Para, Brazil (SELYS, 1859, 1869). The 10 males I examined were collected in February, June, and August. The known distribution is peculiarly linear, 3 points along the Amazon River in Brazil: Manaus, Amazonas State, and Santarem and Belem, Para State.

HELIOCHARIS AMAZONA SELYS, 1853 Figure 2

Heliocharis braziliensis Hagen in SELYS, 1859 — [new synonym]
Heliocharis libera SELYS, 1869 — [new synonym]
Cyanocharis valga NEEDHAM, 1903 — [new synonym]
Neocharis cothurnata FOERSTER, 1906 — [new synonym]
Dicterias umbra RIS, 1918 — [Listed in synonymy by DAVIES & TOBIN, 1984]
Dicterias peruviana NAVAS, 1920 — [Synonymized by SCHMIDT, 1942]
Charitopteryx COWLEY, 1934 — [new synonym]

MORPHOLOGY AND VARIATION

As shown in Table I, a total of 127 specimens (86 & 3, 41 & 9) was examined from 8 countries. Overall ranges in size parameters for males were (mm): total length 46-58, abdomen 35-44, hindwing 27-34; for females 45-55, 33-41, 29-35. Measurements from the literature were similar. In Table I a trend can be seen toward slightly smaller size from west to east in both males and females. As in most Odonata, abdomens of females were a little shorter, but wings were a little longer, than in males. This is well shown in the hindwing/abdomen ratios of males, 71-84%, compared with 81-97% in females.

SELYS (1853) stated that the nodus was far beyond the middle of the wing, but in 1854 he changed that to the middle of the wing. The overall ratios of base to nodus length relative to hindwing length in my sample were 40-47% in males, 39-45% in females. Thus the nodus actually lies proximal to the middle of the wing, and the position of the nodus in the hindwing varied by 8% in males, 7% in females.

As shown in Table II, some specimens lacked midbasal crossveins, others had up to 6 such crossveins. Several specimens had 2, 3, or 4 midbasal crossveins in different wings of the same individual. Partial midbasal crossveins were present in at least one wing (data not shown in Table II) in 11% of specimens from Peru and Rondonia, Brazil, 44% in the remainder from Brazil, and 57% from Paraguay. Most partial crossveins were present in specimens which also had complete crossveins. This variation in midbasal crossveins is greater than in any other odonate known to me, and is a primary reason for so many synonyms of H. amazona.

Table I

Variation in size parameters in *Heliocharis amazona* — [N = number of specimens examined; — TL = total length from labrum to tips of cerci in mm; — AB = length of abdomen from thorax to tips of cerci in mm; — HW = straight-line length of hindwing from base of costa to tip in mm; — HW/AB = length of hindwing relative to length of abdomen in %; — Nodus/HW = ratio of distance from base of costa to nodus relative to length of hindwing in %. — SW Brazil = Rondonia State; — E Brazil = Amazonas, Para, and Minas Gerais States]

Locality	Sex	N .	TL	AB	HW	HW/AB	Nodus/HW
Ecuador	ð	19	51-58	39-44	28-34	74-83	41-45
	φ	8	49-55	37-41	32-35	85-90	40-42
Peru	ð	20	52-57	38-43	30-34	74-83	41-44
	φ	7	50-55	37-41	32-35	83-89	40-42
SW Brazil	ð	22	46-56	35-41	27-33	76-84	40-47
	φ	14	45-52	33-39	29-34	85-97	39-44
E Brazil	8	8	48-54	36-40	28-30	75-81	41-47
	φ	8	48-50	35-37	29-32	84-89	41-45
Paraguay	ð	6	47-53	35-39	28-30	77-81	40-43
	φ	1	51	38	33 -	87	40
Venezuela	ð	4	54-57	40-42	29-30	71-75	41-43
Guyana	Q	1	53	39	33	85	40
Surinam	ð	3	50-53	38-40	29-30	75-76	40-41
	φ	1	49	37	33	89	40
French Guiana	na & 4 53-56 3	39-41	29-31	73-80	40-43		
	ç	1	49	37	30	81	40

Table II

Variation in venation in *Heliocharis amazona* — [N = number of male and female specimens combined at each locality (for relative numbers of each, see Tab. I); — MBX = range in number of midbasal crossveins; — %1+ = percent of specimens with 1 or more midbasal crossveins in at least 1 wing; — QX = range in numbers of crossveins in quadrangle; — %2+ = percent of specimens with 2 or more quadrangular crossveins in at least 1 wing; — % 2 Rows = percent of specimens with 2 rows of cells instead of 1 row posterior of Cu2 in at least 1 wing]

Locality	N	MBX	%1+	QX	%2+	%2 Rows
Ecuador	27	0	0	1-2	26	7
Peru	27	0-1	19	1-2	52	15
SW Brazil	36	0-1	11	1-2	36	0
E Brazil	16	0-6	81	1-2	69	6
Paraguay	7	1-4	100	0-1	0	0
Venezuela	4	0	0	1-3	100	25
Guyana	i	0	0	2	100	0
Surinam	4	0-1	25	1-3	100	25
French Guiana	5	0	0	1-2	100	20

One quadrangular crossvein was usual in the western part of the range of *H. amazona*, but 2 crossveins were common (Tab. II). In the Guianan area 2 quadrangular crossveins was standard. Rare variations were: no quadrangular

crossveins (1 wing Paraguay) or 3 quadrangular crossveins (1 wing Venezuela, 2 wings Surinam). This variation encompasses that of *Neocharis* and *Charitopteryx* (see below). The number of quadrangular crossveins does not seem to be correlated with the number of midbasal crossveins. This is seen most clearly in Paraguayan specimens, all of which had 1 or more midbasal crossveins, but none had 2 or more quadrangular crossveins.

Subcostal crossveins proximal to the first thickened antenodal varied from 1-4 in each wing, with no apparent geographical pattern. Costal crossveins proximal to the first thickened antenodal were generally rare, but were present in 8/9 specimens from Igarape Assu, Para, Brazil.

Table II shows that usually only 1 row of cells is present posterior to Cu2, but a few specimens from most countries had 2 rows 4 or more cells long (total 9 \Im , 2 \Im), a variation toward *Cyanocharis* (see below). The extra row of cells was most often present in one or both hindwings.

In 6 males (1 Ecuador, 4 Brazil, 1 Paraguay) M1-2 was bowed anteriorly more than usual so as to contact R, duplicating the normal condition in *D. atrosanguinea*. Because of the lengthwise fluting of the wings, a photograph or other perpendicular view of a wing may show these veins in contact, when in reality they are separate; an oblique view is necessary to verify this character.

The sectors of the arculus are usually separate at their origin, but they originate at a point in some wings.

In spite of the variable venation within and between localities, *H. amazona* showed remarkably little differentiation in coloration or body morphology over its vast range. However, the following tendencies, which were not quantified, were noted. Guianan specimens (Venezuela to French Guiana) had wider and more distinct brown thoracic stripes; males had shorter terminal penis lobes, and in lateral view narrower posterior hamules. Ecuadorian specimens usually had small postoccipital tubercles, and the males usually had black labra. Some specimens from Peru and western Brazil also had postoccipital tubercles and dark labra (but latter can be an artifact of preservation).

Tenerals of *H. amazona* are mostly olive green, males develop a mostly blue abdomen. The pronotum and interalar sclerites may be either green or blue in both sexes. Eyes of males in life black dorsally, green ventrally, of females brown dorsally, yellow ventrally (Rondonia, Brazil).

One male (Brazil, Minas Gerias, Santana do Riacho, base of Serra do Cipo, Dec. 1975, coll. A.B.M. Machado, R. Garrison collection) differed from other specimens, perhaps at the subspecific level. It had the head and thorax marked with blue instead of green, and no mesepimeral brown stripe. This male also had 2 rows of cells posterior to Cu2 in 3 wings (1 wing missing) and short penis horns.

REMARKS ON TAXONOMY

Heliocharis was described by SELYS (1853), and amplified by SELYS (1854). The major difference in venation from Dicterias is the course of M2, which in Heliocharis diverges at a small angle from M1, leaving room between those veins for only one intercalated sector proximal to the pterostigma. In Dicterias, M2 diverges at a wider angle, allowing space for 3 intercalated sectors proximal to the pterostigma.

SELYS (1853) described *Heliocharis amazona* from 1 male, thought to be from Bolivia, which had 4 midbasal crossveins. SELYS (1854) expanded the description, and illustrated a forewing and abdominal segments 9-10. He explained in the figure captions that the drawings were rapid sketches made while he was in London. Thus both descriptions were from notes, without the holotype at hand. SELYS (1869) later admitted that the wing figure was inaccurate, but unfortunately later authors, particularly NEEDHAM (1903a), FOERSTER (1906), and RIS (1918) took the drawing at face value and erected new species and even new genera on that basis. The holotype male was from the Ega River, a tributary of the Amazon, which HAGEN (1861) stated is in Brazil rather than Bolivia. I believe the Ega River is now known as the Rio Tefe, Amazonas State, Brazil, 3.35 S, 64.47 W. The location of the holotype, apparently originally at the British Museum because the species was listed by WALKER (1853, as *Dicterias amazona*), is not known (S. Brooks, pers. comm.).

If one accepts the synonymy given in the present paper, male *H. amazona* have been described relatively extensively by SELYS (1854) in French, NEEDHAM (1903a) in English, and by FOERSTER (1906) and RIS (1918) in German. Female *H. amazona* were described briefly by SELYS (1869), by NAVAS (1920), and much more completely by CALVERT (1948).

One or more wings of *H. amazona* have been illustrated by SELYS (1854), CALVERT (1909), MUNZ (1919), TILLYARD & FRASER (1939), and FRASER (1957). SELYS (1854) sketched the male cerci, the penis was illustrated by KENNEDY (1919, 1920), and a leg was figured by COWLEY (1937).

The larva of *H. amazona* was described by GEIJSKES (1986) and by SAN-TOS & COSTA (1988). Both descriptions were well illustrated. All of these authors considered the larva close to *Hetaerina* of the Calopterygidae, but Geijskes also noted that the mandibles were 2-branched as in the Megapodagrionidae. DE MARMELS (1989) pointed out the similarities of 6 characters between the larva of *H. amazona* and *Megapodagrion venale* (Selys).

Heliocharis braziliensis was described from probably 1 male at a time when only the holotype male of H. amazona was known. SELYS' (1859) brief description listed these differences from amazona: abdomen 39 instead of 35 mm, occiput more spotted, thoracic stripes longer, 1 midbasal crossvein instead of 4, 3 rows of postcubital cells distally instead of 1 row. All of these characters are

within the range of variation of *H. amazona*. The holotype male of *H. braziliensis* was from Bahia, eastern Brazil, and should be in the Berlin Museum.

Heliocharis libera was described by SELYS (1869) from probably 1 male and 1 female taken at Santarem, Para, Brazil. Differences listed from H. amazona were: no midbasal crossveins, nodus more proximal, wings more slender, forewing antenodals 19-20 instead of 16, forewing postnodals 22-23 instead of 15. SELYS (1869) added: "This is probably only a race, possibly also an aberration of amazona,...". In the same paper, Selys recorded a male H. amazona with 4 midbasal crossveins from the same locality. HAGEN (1875) listed H. libera as a probable synonym of H. amazona. SCHMIDT (1942) listed it as a subspecies of H. amazona, and RACENIS (1959) repeated Schmidt's listing. FRASER (1946, 1948) used libera as a full species. PAULSON (1977) listed libera as a synonym of amazona, but later (1985) used libera. I view libera as a strict synonym of amazona because its characters fall within the variation of amazona. The type specimens of H. libera are presumably in the Selys collection in Brussels.

Cyanocharis valga, known only from the holotype male, seems to be an aberrant specimen of Heliocharis amazona. NEEDHAM (1903a) described it from Poco Grande, Brazil, at a time when only 4 males of Heliocharis were known, and when the only available figure of a Heliocharis wing was SELYS' (1854) sketch. The description of C. valga agrees with those of H. amazona, but the holotype of valga had no midbasal crossveins, M1-2 was bowed anteriorly to touch R for a short distance, and there were 3 rows of cells between Cu2 and the hind margin of the wing. The first two characters are encompassed by variations of H. amazona, but the third is different. I have not seen any other H. amazona with 3 rows of cells posterior to Cu2, but as noted above a few specimens had 2 such rows in one or more wings, though most had only 1 row. BICK & BICK (1990, Odonatologica 19: 117-143) found similar variation in 3 species of Cora (Polythoridae) each of which had 2 or 3 rows of cells posterior to Cu2. The type locality of Cyanocharis valga is unknown, for there are at least 4 "Poco Grande" in Brazil, all in different states. However, Poco Grande in Sao Paulo State (24.55 S, 49.03 W) is most likely since Adolph Hempel, the collector, did most of his collecting in Sao Paulo State. The wings of C. valga have been illustrated by NEEDHAM (1903b), MUNZ (1919), and TILLYARD & FRASER (1939). These illustrations differ in detail and may be of different wings. FRASER (1957) repeated the figure of TILLYARD & FRASER (1939). The holotype of C. valga was in the Cornell University collection, Ithaca, New York, but is apparently lost (J. Liebherr, pers. comm.).

FOERSTER's (1906) description of *Neocharis cothurnata*, based on 2 males from Surinam, separated *Neocharis* from *Heliocharis* because the sectors of the arculus originated at one point, and midbasal crossveins were absent, but these characters are within the range of variation in *Heliocharis*. The only "new" character given for *N. cothurnata* was 2 quadrangular crossveins, but this

number is common in *Heliocharis amazona*. RIS (1918) synonymized *Neocharis* with *Dicterias* because he thought that SELYS (1869) had reduced *Heliocharis* to a subgenus of *Dicterias* (see following discussion of *D. umbra*). This incorrect synonymization was followed by CALVERT (1948) and DAVIES & TOBIN (1984). The syntypes of *N. cothurnata* are at the University of Michigan, Ann Arbor (R. Garrison, pers. comm.).

Dicterias umbra was placed in Dicterias because RIS (1918) misinterpreted SELYS' (1869) change in classification to be a reduction of Heliocharis to a subgenus of Dicterias. Selys combined his "grands genres" (equal to a modern subfamily) Dicterias and Heliocharis into one category, Dicterias; his "sous--genres" (equal to modern genera) remained as Dicterias and Heliocharis. The change in SELYS' classification at the subfamily level but not at the generic level can be seen by comparing his early and late classifications (1853, p. 6; 1873, p. 44). In addition, the only difference RIS (1918) saw between Dicterias and Heliocharis was the presence of midbasal crossveins in the latter, so he did not recognize Heliocharis even as a subgenus. Ris reached this incorrect conclusion partly because of SELYS' (1854) inaccurate wing drawing of Heliocharis. Thus RIS (1918) for at least two reasons should have placed umbra in Heliocharis rather than in Dicterias. It is convenient to mention here that FRASER (1946) also misinterpreted SELYS' (1869) change in classification, but Fraser considered Heliocharis and Dicterias to be distinct genera, with Dicterias more evolutionarily advanced.

Dicterias umbra was described (RIS, 1918) from a male from Villavicencio, central Colombia, and a female from Bom Jesus de Itabapoana, Rio de Janeiro State, eastern Brazil. The wings of both specimens were illustrated; those of the female show a tendency to 2 rows of cells posterior to Cu2, a variation in the direction of Cyanocharis valga. SCHMIDT (1942) stated that D. umbra was probably a synonym of Heliocharis amazona, and DAVIES & TOBIN (1984) list D. umbra, I think correctly, as a synonym of H. amazona. The holotype male and allotype female of D. umbra are in the Ris collection, Senckenberg Museum, Frankfurt, Germany.

Dicterias peruviana Navas, 1920 was described from 1 female from the Rio Ucayali, Contamana, Peru. NAVAS (1920) illustrated the base of a forewing, and COWLEY (1937) illustrated a male leg ascribed to *D. peruviana*. SCHMIDT (1942), on the advice of Ris in a letter, listed *D. peruviana* as a synonym of *H. amazona*, and RACENIS (1959) followed Schmidt's synonymy. DAVIES & TOBIN (1984) also listed *D. peruviana* as a synonym of *H. amazona*. The holotype female *D. peruviana* should be in the Navas collection, Barcelona, Spain.

COWLEY (1934), noting that *Neocharis* Foerster, 1906 was preoccupied by *Neocharis* Sharp, 1877, a name for a beetle, proposed the new name *Charitopteryx*. Since *Neocharis* Foerster is a synonym of *Heliocharis*, so is *Charitopteryx*.

DAVIES & TOBIN (1984), following CALVERT (1948), incorrectly listed *Charitopteryx* and *Neocharis* as synonyms of *Dicterias*.

BIOLOGY

Egg: I found 2 eggs of *H. amazona* attached to specimens from the Rio Pardo, Rondonia, Brazil. The eggs were 1.75x0.25 mm, yellow, cylindrical, and abruptly conical at the anterior pole.

Larva: SANTOS & COSTA (1988) stated that the larvae move slowly and inhabit the edges of streams varying in size from small creeks to rivers. Probably the larvae cling to roots in the current, as do *Hetaerina* larvae.

Adult: GEIJSKES (1986) reported that: "Isolated imagines are met with along slow flowing bush-creeks, where they are sitting in the shadow on vines and stems of water plants, the wings half spread. They do not rise quickly". I observed in Rondonia, Brazil, that males perched horizontally on overhanging leaves in sunny spots 1-2 m up with the wings outspread, as in most Anisoptera. Males were extremely wary, flushing at a distance of several m. W. Clarke-MacIntyre noted on the envelopes of several taken on the Rio Jatun Yacu, Ecuador: "Wild and hard to catch". Females seemed much less wary than males, and were seen in both sunlight and shade on leaves along the stream, on leaves near the ground, and on twigs of a fallen tree in a clearing.

A male *H. amazona* from Manu, Peru, was collected while eating a 10 mm long tenebrionid beetle *Strongylium* nr *decoratum* Maklin (det. M.C. Thomas, 1990). A male from Arroyo Pindo, San Pedro, Paraguay had a female ceratopogonid fly *Forcipomyia (Pterobosca) incubans* (MacFie) (det. W.W. Wirth, 1990), a common parasite specific to Odonata, on a wing. No mites were present on any specimen.

Nothing is recorded of mating or oviposition in *H. amazona*. Because only 2 of the female *H. amazona* I examined had soiled abdomens, they probably oviposit in clean running water. Also, since the ovipositor and the teeth on it are small, they probably oviposit in soft plant tissues such as decomposed wood.

I examined specimens of *H. amazona* taken in every month of the year, so it has an all year flight season. PAULSON (1985) reported the species in both the dry and wet seasons at Tambopata, Madre de Dios, Peru.

H. amazona occurs throughout the Amazon basin and the Guianas. It or its synonyms have been reported from Brazil, Surinam, Guyana, French Guiana, eastern Venezuela, Colombia, Peru, and northern Argentina. I examined specimens from the countries listed in Table 1, adding Paraguay and Ecuador to the list above. The species has thus been recorded from every country in South America except Bolivia, Chile, and Uruguay. H. amazona probably occurs in Bolivia, but is not expected in Chile or anywhere west of the Andes. It occurs up to an elevation of 1000 m in Ecuador.

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ANNOTATED CHRONOLOGICAL BIBLIOGRAPHY

The following list includes every reference to any taxon of the Dicteriadidae known to me. For each publication, the pages where references were made are given in [], and the number of specimens dealt with and any illustrations are stated. The bibliography is chronological so that the reader can see the information available to each author from previous work. The reader should look up citations in the present paper first by year, then by author.

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