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VARIABILITY IN LARVAL CHARACTER STATES USED TO DISTINGUISH BETWEEN SPECIES OF *PANTALA* HAGEN (ODONATA: LIBELLULIDAE)

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ABSTRACT

Despite widespread distributions and abundance, previously published diagnoses of the larvae of the two species of the dragonfly genus *Pantala* often were contradictory or confusing. Morphometric analysis of mensural characters and qualitative analysis of relative character states were used to determine the ability of previously published characterizations to accurately distinguish larvae of the two species. We found that many published characterizations were inaccurate or insufficient, and their use in making species level determinations would result in frequent misidentifications. In distinguishing between the two species, the most useful and reliable characteristic was the palpal setal count. However, in specimens where this count is intermediate, other characteristics may need to be evaluated.

RESUMEN

A pesar de su distribución amplia y su abundancia, las diagnosis publicadas anteriormente de las larvas de dos especies de libélulas del género *Pantala* a menudo son contradictorias o confusas. El análisis morfométrico de los carácteres mensurales y el análisis cualitativo de los carácteres de estado relativos fueron empleados para determinar la abilidad de las caracterizaciones publicadas anteriormente para distinguir las larvas de las dos especies con exactitud. Nosotros encontramos que muchas de las caracterizaciones publicadas fueron inexactas o insuficientes, y su uso para hacer determinaciones a nivel de especie resultarían frecuentemente en identificaciones equivocadas. Para distinguir entre las dos especies, la característica mas útil y confiable es el conteo de las setas del palpo. Sin embargo, en especimenes donde el conteo es intermedio, se necesitan que otras características sean evaluadas.

The genus *Pantala* Hagen is represented worldwide by two species, both of which are widespread and abundant in the United States. Many characters have been used to diagnose the larva of each species and distinguish between them. However, character states attributed to each species frequently have been contradictory among authors, raising questions as to the diagnostic reliability of these characters.

Kennedy (1923) was the first to distinguish between *P. hymenaea* (Say) and *P. flavescens* (Fabricius). Needham (1901) had previously characterized the movable hook of *P. flavescens* as "hardly longer than the teeth." Kennedy described the larva of *P. hymenaea* and distinguished it from Needham's diagnosis of *P. flavescens* on the basis of the moveable hook of the former as "twice as long as the crenulations of the distal edge of the lobe." Lamb (1929) investigated this character and found that the mean ratio of the length of the movable hook to length of the first palpal crenulation was 2.2 in *P. hymenaea* (3 specimens, 1 reared) and 2.6 in *P. flavescens* (8 reared specimens). Musser (1962) examined more specimens than the previous authors (60 *P. hymenaea*, 1 with associated adult; 39 *P. flavescens*, 3 with associated adults) and found the ratios to be 2.0 and 2.5-3.0 for *P. hymenaea* and *P. flavescens*, respectively. However, authors continued to characterize the movable hook of *P. hymenaea* as 2 times as long as the crenulations of the labial palp while characterizing that of *P. flavescens* as less (Byers 1930; Smith & Pritchard 1956; Walker & Corbet 1975; Huggins & Brigham 1982).

Two of the interspecific distinctions that appear most commonly in the modern literature without contradiction were first given by Musser (1962), who stated that the lateral spines of abdominal segment IX were less than three times as long as the basal width in *P. hymenaea*, and at least three times as long in *P. flavescens*. Musser also mentioned a "slight hump midway along" the dorsal margin of the epiproct, and diagrammed the dorsal margin abruptly decurved at a point somewhat beyond midlength in *P. hymenaea*, while characterizing and depicting a straight dorsal margin of the epiproct in *P. flavescens*. Both of these distinctions subsequently have been repeated, and the accompanying diagrams reproduced, in several faunistic treatments (e.g., Walker & Corbet 1975; Huggins & Brigham 1982; Needham et al. 2000). Paulson (1966) also noted that the lateral spines of *P. flavescens* were more elongate than those of *P. hymenaea* but offered no quantification other than that the spines of VIII reach or exceed the apical margin of IX in the former and not the latter.

Palpal setal counts also have been used to characterize each species of *Pantala* and to distinguish between them. *P. flavescens* is generally characterized as bearing 12-14 palpal setae (Needham 1901; Lamb 1929; Needham & Heywood 1929; Byers 1930; Klots 1932; Smith & Pritchard 1956; Musser 1962; Walker & Corbet 1975; Huggins & Brigham 1982) and *P. hymenaea* as bearing 15 (Kennedy 1923; Needham & Heywood 1929; Byers 1930; Klots 1932; Smith & Pritchard 1956; Musser 1962; Walker & Corbet 1975; Huggins & Brigham 1982) or more (Lamb 1929; Klots 1932; Musser 1962). Paulson's (1966) table of palpal setal counts is the only work documenting intraspecific variation and, in *P. flavescens,* he found 14 or fewer setae on at least one palp in all 16 specimens examined (4 reared), but found 15 on a single palp in two specimens, and 16 and 17 on a single palp in one specimen each. In *P. hymenaea*, he also found 16 or more palpal setae on at least one palp in each of 13 specimens examined (1 reared), but found 15 on a single palp in one specimen.

Needham & Westfall (1955) presented two novel characters to distinguish between species of *Pantala*. They characterized the epiproct of *P. flavescens* as longer than the paraprocts, and that of *P. hymenaea* as subequal to the paraprocts. This distinction was adopted by Young & Bayer (1979). Paulson (1966) believed this to be a fairly reliable distinction, but found some specimens of each species to be indistinguishable based on this distinction. Musser (1962) also agreed that this was generally the case, but found measurement of these characters too difficult to reliably quantify and be useful. Needham & Westfall (1955) also distinguished *P. hymenaea* from *P. flavescens* on the basis of a more marked color pattern in the former, which also was adopted by Young & Bayer (1979). Paulson (1966) and Musser (1962) both refuted this distinction as unreliable, yet it appeared again in Needham et al. (2000).

Materials and Methods

A total of 46 specimens of *Pantala* was examined. Of these, 27 specimens were *P. hymenaea*: 23 from Missouri (16 reared exuvial specimens, 7 final instars) and 4 from California (all reared exuvial specimens). Nineteen specimens of *P. flavescens* were examined, including 12 from Missouri (1 reared exuvial specimen, 11 final instars) and 7 from Florida (all reared exuvial specimens). Missouri specimens are deposited in the Enns Entomology Museum, University of Missouri, Columbia, Missouri; all other specimens are in the collection of J. C. Abbott.

All measurements were performed with an ocular micrometer on the strict dorsal aspect of the specimen. Measurements were rounded to the nearest 0.04 mm. The lengths of lateral spines were measured on one side of the specimen, along a line parallel to the long axis of the body, from the posterior margin of the segment immediately adjacent to the base of the spine to the level attained by the tip of the spine. The basal width of a lateral spine was measured along a tangent perpendicular to the long axis of the body, from the point on the posterior margin of the segment immediately adjacent to the base of the spine to the lateral margin of the segment. Mid-dorsal segment length was measured from the anterior to the posterior margin of the tergite. Palpal setae were counted on each palp.

Other characteristics were evaluated qualitatively. Specimens were examined in lateral view to determine if the apex of the epiproct exceeded the apices of the paraprocts. The color pattern was considered distinct or indistinct. Due to nonuniform telescoping reported in the abdomens of larval and exuvial specimens (see Calvert 1934; Huggins & Harp 1985), the posteriormost distance on segment IX attained by the lateral spines of VIII was not evaluated. Also, precise measurements of the relative lengths of the moveable hook and crenulations of the labial palps were very difficult to obtain without damaging the specimens, and were evaluated comparatively between species. The convexity of the dorsal margin of the epiproct in lateral view also was evaluated comparatively.

Material examined.—CALIFORNIA: Fresno Co., Enterprise Canal E. Clovis, 1 Nov 1976, S. W. Dunkle (exuviae of 4 reared *P. hymenaea*); FLORIDA: Alachua Co., NE Gainesville, Nov 1975, S. W. Dunkle (exuviae of 6 reared *P. flavescens*); same data, Austin Cary Fishpond, coll. 22 Sep 1978, emerged 23 Sep 1978, S. W. Dunkle (exuviae of 1 reared *P. flavescens*); MISSOURI: Audrain Co., R. M. White II Conservation Area, Sep 9, 1998, BHPL & N. Whiteman (2 *P. flavescens* larvae); Benton Co., Lost Valley Fish Hatchery, 6 Oct 2000, L. Trial (exuviae of 3 unreared, 1 larval *P. flavescens*); Boone Co., Ditch near Vet. School, University of Missouri campus, 30 Jul 2001, BHPL (exuviae of 1 reared, 3 larval *P. hymenaea*); Christian Co., SW Nixa, ca. 200 gallon stock tank, 15 Aug 2001, BHPL (exuviae of 11 reared *P. hymenaea*); Jackson Co., Jacomo Lake, no date, S. Thewke (1 *P. flavescens* larva); Pemiscot Co., University of Missouri Lee Farm, rice paddy, 25 Jul 2001, BHPL & C. Luppens, (exuviae of 1 reared, 1larval *P. flavescens*; exuviae of 3 reared, 4 larval *P. hymenaea*); Texas Co., 4 mi. S Simmons, 4 Oct 1972, S. Thewke (3 *P. flavescens* larvae).

Results

On average, the lateral spines were longer in *P. flavescens* and broader in *P. hymenaea* (Table 1). However, considerable interspecific overlap existed in each of these measurements. Interestingly, less

TABLE 1. CHARACTER MEASUREMENTS (MM) AND RATIOS OF SPECIMENS OF *PANTALA HYMENAEA* AND *P. FLAVESCENS*. ITALICIZED VALUES OVERLAP BETWEEN SPECIES.

Species	Specimen	Length spine 9	Width spine 9	Length spine 8	Mid-dorsal length 8	Palpal setae	Length/width spine 9	Length spine 8/ width spine 9	Mid-dorsal length 8/ length spine 8
P. hymenaea	1	*2.64*	0.84	*1.36*	1.52	16	3.14	1.62	1.12
	2	*2.60*	0.84	*1.32*	1.68	17/16	3.10	1.57	1.27
	3	*2.64*	0.96	*1.48*	1.64	16	2.75	1.54	1.11
	4	*2.40*	0.92	*1.40*	1.60	17	2.61	1.52	1.14
	5*	*2.60*	0.84	*1.28*	1.60	16/17	3.10	1.52	1.25
	6*	*2.56*	0.84	*1.32*	1.48	16/17	3.05	1.57	1.12
	7*	*2.28*	0.84	1.12	1.60	16	2.71	1.33	1.43
	8*	*2.56*	0.84	*1.48*	1.56	17/18	3.05	1.76	*1.05*
	9*	*2.76*	*0.80*	*1.48*	1.60	17	*3.45*	1.85	1.08
	10*	*2.36*	0.84	*1.24*	1.48	17/18	2.81	1.48	1.19
	11*	*2.44*	*0.76*	*1.32*	1.48	16/17	3.21	1.74	1.12
	12	*2.08*	*0.80*	1.04	*1.44*	17	2.60	1.30	1.38
	13	*2.56*	0.88	*1.24*	1.60	16	2.91	1.41	1.29
	14	*2.20*	0.92	*1.24*	1.48	16	2.39	1.35	1.19
	15	*2.12*	*0.72*	1.08	1.48	*15*/17	2.94	1.50	1.37
	16	*2.48*	0.92	*1.32*	1.56	16/17	2.70	1.43	1.18
	17	*2.28*	*0.80*	1.08	1.48	17	2.85	1.35	1.37
	18	*2.52*	*0.72*	*1.40*	1.52	16	*3.50*	*1.94*	*1.09*
	19	*2.20*	*0.80*	*1.16*	1.48	17	2.75	1.45	1.28
	20	*2.48*	0.84	*1.32*	1.52	16/17	2.95	1.57	1.15
	21	*2.44*	*0.80*	*1.24*	1.60	16/17	3.05	1.55	1.29
	22	*2.40*	*0.80*	*1.20*	1.48	16/17	3.00	1.50	1.23
	23	*2.72*	0.92	*1.52*	1.56	17/18	2.96	1.65	*1.03*
	24	*2.40*	0.88	*1.32*	1.56	17	2.73	1.50	1.18
	25	*2.48*	0.96	*1.28*	1.48	16	2.58	1.33	1.16
	26	*2.20*	0.88	1.04	1.56	16/17	2.50	1.18	1.50
	27	*2.40*	0.84	*1.20*	1.48	17	2.86	1.43	1.23
Mean		2.41	0.84	1.26	1.53		2.90	1.51	1.23
S.E.		0.18	0.06	0.14	0.06		0.27	0.17	0.12

*Larval specimen or unreared exuviae.

TABLE 1. (CONTINUED) CHARACTER MEASUREMENTS (MM) AND RATIOS OF SPECIMENS OF *PANTALA HYMENAEA* AND *P. FLAVESCENS*. ITALICIZED VALUES OVERLAP BETWEEN SPECIES.

Species	Specimen	Length spine 9	Width spine 9	Length spine 8	Mid-dorsal length 8	Palpal setae	Length/width spine 9	Length spine 8/ width spine 9	Mid-dorsal length 8/ length spine 8
P. flavescens	1	*2.40*	0.56	*1.28*	1.36	13	4.29	2.29	*1.06*
	2	*2.20*	0.56	*1.28*	1.28	13	3.93	2.29	1.00
	3	*2.24*	0.60	*1.32*	1.36	13	3.73	2.20	*1.03*
	4	2.04	0.56	*1.16*	1.24	13/14	3.64	2.07	*1.07*
	5	*2.24*	0.64	*1.20*	1.32	13	*3.50*	*1.88*	*1.10*
	6	*2.44*	*0.72*	*1.44*	1.28	13/14	*3.39*	2.00	0.89
	7	2.80	0.68	1.56	*1.44*	14	4.12	2.29	0.92
	8*	*2.48*	*0.72*	1.56	*1.52*	14	*3.44*	2.17	0.97
	9*	*2.72*	*0.72*	*1.48*	*1.44*	14	3.78	2.06	0.97
	10*	*2.48*	0.64	*1.40*	1.40	13	3.88	2.19	1.00
	11*	2.92	*0.72*	1.80	*1.44*	13/14	4.06	2.50	0.80
	12*	3.00	*0.80*	1.64	*1.44*	14/*15*	3.75	2.05	0.88
	13*	2.88	*0.80*	1.76	*1.44*	14	3.60	2.20	0.82
	14*	2.80	*0.72*	1.72	1.40	14	3.89	2.39	0.81
	15*	2.80	0.68	1.84	1.40	14	4.12	2.71	0.76
	16*	*2.48*	0.56	*1.32*	1.28	13	4.43	2.36	0.97
	17*	*2.52*	0.68	*1.44*	1.36	14	3.71	2.12	0.94
	18*	*2.72*	0.68	*1.52*	1.32	14	4.00	2.24	0.87
	19	*2.52*	0.64	*1.52*	1.40	*15*	3.94	2.38	0.92
Mean		2.56	0.67	1.49	1.37		3.85	2.23	0.94
S.E.		0.27	0.08	0.20	0.07		0.28	0.19	0.10

*Larval specimen or unreared exuviae.

overlap existed in the mid-dorsal length of abdominal segment VIII. In fact, the smallest measurement in *P. hymenaea* (1.44 mm) was equal to the largest in *P. flavescens,* although this value was represented in 5 *P. flavescens* specimens.

Length to width ratios of the lateral spines exhibited less overlap than did absolute measurements of these characters. The length to width ratio of the spine of abdominal segment IX of three (16%) specimens of *P. flavescens* overlapped that of two (7%) of *P. hymenaea* (Fig. 1). However, this overlap occurred at ratios considerably higher than 3.00. In fact, values greater than 3.00 were observed in 10 (37%) specimens of *P. hymenaea* and the minimum value observed in *P. flavescens* was 3.39.

The ratio of the length of the lateral spine of abdominal segment VIII to the basal width of the spine of IX yielded even less overlap than did the length/width ratio of spine IX. The value of this character overlapped in only one specimen each of *P. flavescens* (5%) and *P. hymenaea* (4%). The ratio was less than 2 in all specimens of *P. hymenaea*, and greater than 2 in all but one specimen of *P. flavescens*. The ratio of the length of the spine of abdominal segment VIII to the mid-dorsal length of that segment showed greater overlap; the ratios in four *P. flavescens* specimens overlapped those in three *P. hymenaea*.

The larvae examined displayed a remarkable lack of symmetry in the number of palpal setae on the left and right palp of individual specimens. However, the total number of palpal setae showed no overlap between species (Fig. 2). Applied to each palp, the characteristic of 14 or fewer palpal setae correctly identified 17 (89%) *P. flavescens* larvae. Fifteen palpal setae on each palp was not characteristic of any *P. hymenaea* specimen, however 15 or more correctly identified all specimens, and 16 or more characterized all but a single palp of one specimen. No specimen of *P. flavescens* bore more than 15 palpal setae on either palp. Conversely, all *P. hymenaea* specimens bore 16 or more setae on at least one palp.

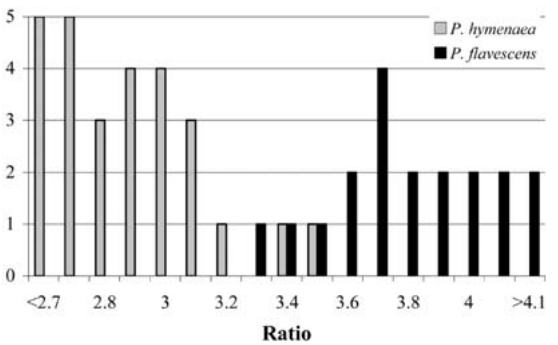

Fig. 1. Frequency of expression of length/width ratios of spine 9 in specimens of *Pantala*

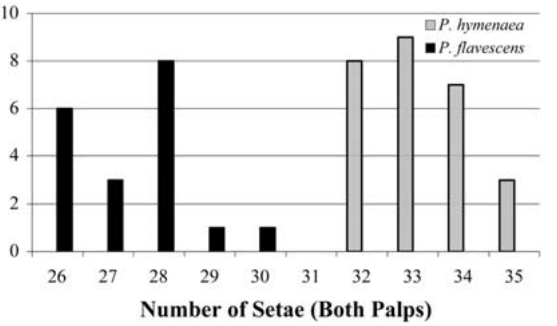

Fig. 2. Frequency of expression of palpal setal counts in specimens of *Pantala*

Discussion

This analysis clearly reveals the inadequacy of existing interpretations of the distinction between species of larval *Pantala*. These results indicate that the possession of 15 or fewer palpal setae on each palp will distinguish *P. flavescens* larvae from *P. hymenaea*, although two specimens of *P. flavescens* examined by Paulson (1966) vitiate this characterization. If one includes the stipulation that *P. flavescens* specimens bearing greater than 15 palpal setae on one palp bear fewer than 15 on the other, this characterization is not violated. This distinction might be best expressed as the sum of palpal setae from both palps (see Fig. 2). Thirty or fewer setae is characteristic of *P. flavescens* and 32 or more of *P. hymenaea*. This characterization does not exclude Kennedy's (1923) original description of the larva of *P. hymenaea* and characterization based upon it. However, Lamb (1929) examined Kennedy's *P. hymenaea* material, and reported that the specimens bore at least 17 palpal setae. It is not known if she examined the same specimens from which the description was prepared.

As noted by Musser (1962) and Paulson (1966), the lateral spines of *P. hymenaea* are generally stouter than those of *P. flavescens*. However, it is clear from this analysis that the characterization of *P. hymenaea* larvae as bearing lateral spines on abdominal segment IX less than three times as long as the basal width is inadequate. The maximum value of this ratio found in *P. hymenaea* was actually 3.50, slightly greater than the minimum value in *P. flavescens*. Our results indicate that the possession of lateral spines on segment VIII that are less than two times as long as the basal width of the lateral spines on segment IX in *P. hymenaea* and greater than two times in *P. flavescens* is a more reliable quantification of the difference in the form of lateral spines between the species.

The characterization of the moveable hook of *P. flavescens* as less than twice as long as the crenu-

lations of the labial palp is clearly erroneous. The specimens examined generally agreed with the assessments of Lamb (1929) and Musser (1962) that the moveable hook of *P. flavescens* is longer than that of *P. hymenaea* relative to the length of the crenulations on the labial palp. It is likely that all characterizations to the contrary are derived from Kennedy's (1923) distinction of larvae of *P. hymenaea* from Needham's (1901) diagnosis of the larvae *P. flavescens*. However, Needham probably offered the characterization of the moveable hook as "hardly longer than the teeth" as an obvious distinction from the long moveable hooks of species of *Tramea*, and not as an absolute measurement.

We found the decurvature of the dorsal margin of the epiproct in lateral view to be a highly subjective and unreliable character to distinguish between species. Although the dorsal margin of the epiproct was generally more convex in *P. hymenaea* (Fig. 3A), rarely was the decurvature as abrupt or as near the apex as figured by Musser (1962). Also, the dorsal margin of the epiproct of *P. flavescens* was often distinctly convex (Fig. 3B) and in no specimen was it as straight as figured by Musser (1962).

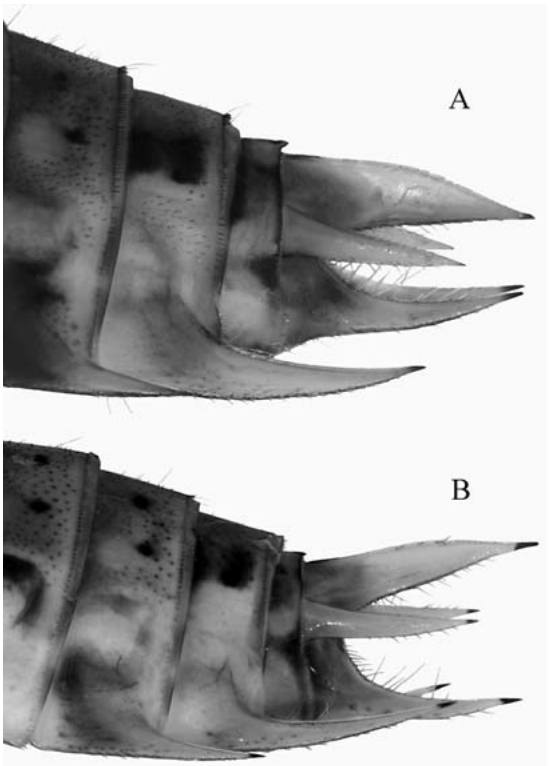

Fig. 3. Lateral view of posterior abdominal segments of (A) *Pantala hymenaea* and (B) *Pantala flavescens* (epiproct is uppermost appendage)

Our evaluation of relative lengths of epiprocts and paraprocts is in accord with those of Musser (1962) and Paulson (1966). Specifically, the distinction was obvious in many specimens, but unclear for several specimens of each species. We also agree with these authors that there is no clear distinction in the intensity of pigmentation. In fact, the color pattern was distinct in all larvae examined, and remained apparent in preserved exuviae.

All specimens possessed spine like dorsal hooks on abdominal segments II and III, and on all but one *P. flavescens*, IV as well. Our results corroborate those of Westfall & Tennessen (1996), who also noted the presence of dorsal hooks on abdominal segments II-IV in both species of *Pantala*. This obviates the erroneous characterization of the genus as lacking dorsal hooks (e.g., Needham & Heywood 1929; Byers 1930; Needham & Westfall 1955; Smith & Pritchard 1956; Needham et al. 2000), the independent characterization of *P. flavescens* as lacking dorsal hooks (Needham 1901; Byers 1930; Walker & Corbet 1975), and the erroneous distinction of *P. hymanaea* from *P. flavescens* on this basis (Daigle 1992). This confusion may be traced to the original description by Cabot (1890) who made no mention of dorsal abdominal hooks.

It seems likely, due to intraspecific variation and interspecific similarity, that no single characteristic will reliably distinguish all larval specimens of *Pantala*. We do agree, however, with the assessment of Paulson (1966) that by evaluating several distinguishing characteristics, almost all specimens can be correctly determined. The simplest characteristic to evaluate is the palpal setal count. Evaluation of this character requires no precise measurement and can be performed without an ocular micrometer. Specimens with 14 or fewer palpal setae on each palp are assuredly attributable to *P. flavescens*, while those bearing 16 or more are attributable to *P. hymenaea*. Specimens bearing 15 or more palpal setae on one palp and 15 or fewer on the other are best identified with an alternate distinction. From this analysis, it appears that lateral spines on segment VIII greater than twice as long as the basal width of the lateral spines on IX is a reliable characterization of *P. flavescens*, and a ratio less than 2 is characteristic of *P. hymenaea*.

We hope that this evaluation of distinguishing characteristics will prompt others to more carefully examine their specimens of *Pantala*. Discrepancies between actual specimens and published characteristics are unacceptable in a genus comprising such ubiquitous, abundant, and easily reared species. We urge researchers to report the state of characters found in other regions so that the extent of variation found throughout the ranges of these widespread species can be documented.

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