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Diagnostic Efficacy of Morphological Characters of Larval *Tramea Lacerata* Hagen and *Tramea Onusta* Hagen (Odonata: Libellulidae) in the Prairie Region of Missouri

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DIAGNOSTIC EFFICACY OF MORPHOLOGICAL CHARACTERS OF LARVAL *TRAMEA LACERATA* HAGEN AND *TRAMEA ONUSTA* HAGEN (ODONATA: LIBELLULIDAE) IN THE PRAIRIE REGION OF MISSOURI

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ABSTRACT

Distinguishing among species of larvae of the dragonfly genus *Tramea* historically has been problematic, largely due to conflicting characterizations of the larvae of *T. lacerata* Hagen and *T. onusta* Hagen (Odonata: Libellulidae) in the literature. The various systematic treatments usually focused on relative lengths of morphological characters to distinguish the species, but often contradicted one another and themselves as to what the diagnostic values actually were. We traced much of the confusion back to errors in the original larval description of *T. onusta*. We used morphometric analyses to determine the efficacy of previously published characterizations to distinguish between the larvae of *T. lacerata* and *T. onusta*. Previous characterizations, especially those involving relative lengths of the caudal appendages, were generally found to be inadequate for distinguishing larvae of the two species. The most reliable characteristic for distinguishing the two species was found to be the length of the epiproct relative to the length of the paraprocts.

Distinguishing among species of larval *Tramea*, especially those of *T. lacerata* Hagen (Odonata: Libellulidae) from those of *T. onusta* Hagen, historically has been very difficult. Needham and Heywood (1929) did not attempt diagnoses or a larval key and warned, "The nymphs of North American forms seem to be lacking in good specific characters." However, subsequent researchers preparing larval keys to *Tramea* seldom mentioned the unreliability of the characters they used. A notable exception is Needham et al. (2000) who stated that their larval key, based on that of Irinue de Souza et al. (1999), which is, in turn, based largely on that of Byers (1927), was "…tentative, as the relative lengths of the caudal appendages and antennal segments apparently are more variable than previously supposed."

One of the characters most commonly used for distinguishing larval *T. onusta* and *T. lacerata* is length of the cerci relative to the epiproct. However, there is little agreement in the literature on the actual state of this character. The taxonomic keys of Needham and Westfall, Jr. (1955), Smith and Pritchard (1956), Young and Bayer (1979), and Daigle (1992) characterized *T. lacerata* as having cerci 0.8 times as long as the epiproct and *T. onusta* with cerci 0.9 times as long as the epiproct. Musser (1962) roughly agreed, giving the ratios as 0.7 for *T. lacerata* and, based on one specimen also used by Byers (1927), 0.875 for *T. onusta*. In the key and larval diagnoses of Walker and Corbet (1975), the ratios were given as about 0.7 or less for *T. lacerata* and about 0.8 or more for *T. onusta*. In the original larval description of *T. onusta*, Byers (1927) gave the absolute lengths of the cerci and epiproct as 2 mm and 2.5 mm, respectively, which yields a ratio of 0.8. However, he gave the ratio of the lengths of the cerci to epiproct as 0.67. Inexplicably, he characterized the cerci as longer than the epiproct for both *T. onusta* and *T. carolina* in couplet two of the accompanying key to species of larval *Tramea*, but cited the cerci to epiproct length ratio of 0.8 for *T. onusta* in

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couplet three. Irinue de Souza et al. (1999) adopted the ratio of 0.67 to characterize the larva of *T. onusta*.

Another commonly confused character used to diagnose the genus *Tramea* is the ratio of epiproct length to paraproct length. The character state of epiproct shorter than paraprocts was used to distinguish larvae of *Tramea* from those of *Pantala* Hagen in several generic keys (e.g., Needham and Westfall, Jr. 1955, Daigle 1992, Westfall, Jr. and Tennessen 1996). The original larval description of *T. lacerata* (Cabot 1890) indicated that the epiproct is shorter than the paraprocts, as did the larval diagnosis of Garman (1927). The original larval description of *T. onusta* and accompanying key (Byers 1927) indicated that this is also the case in *T. onusta*, giving the absolute length of the paraprocts as 3 mm, and an epiproct to paraproct ratio of 0.83. However, Walker and Corbet (1975) presented confounding characterizations by using the state of epiproct longer than the paraprocts to characterize *T. lacerata* in the larval diagnosis and both *T. lacerata* and *T. onusta* in the key to species, while using the state of epiproct shorter than paraprocts to characterize the genus in the generic diagnosis and *T. onusta* in the larval diagnosis. Needham et al. (2000) also characterized *T. onusta* larvae as having an epiproct longer than the paraprocts. By attributing a cercus to epiproct length ratio of 0.67 and a cercus to paraproct length ratio of 0.80, the species key of Irinue de Souza et al. (1999) indirectly attributed an epiproct to paraproct ratio of 1.2 to *T. onusta*.

The states of characters other than caudal appendages have been used by some authors to distinguish larval *T. lacerata* from *T. onusta*. The fourth antennal segment half as long as the third has been attributed to *T. lacerata* and two-thirds as long to *T. onusta* with little contradiction (Byers 1927, Smith and Pritchard 1956, Walker and Corbet 1975, Needham et al. 2000). Huggins and Brigham (1982) used the state of fourth antennal segment $\leq$0.66 times (mean = 0.58) the length of the third to distinguish *T. lacerata* from *T. carolina* (L.). Also, lateral spines of abdominal segment VIII less than 0.8 times as long as those of IX have been attributed to *T. lacerata* versus nearly as long in *T. onusta* (Daigle 1992). Huggins and Brigham gave this ratio as less than 0.88 (mean = 0.79) in both *T. lacerata* and *T. carolina* and 0.88 or more in *T. onusta* (mean = 0.92). Finally, lateral spines of abdominal segment VIII incurving has been used to characterize both *T. lacerata* and *T. onusta* (Needham and Westfall, Jr. 1955, Walker and Corbet 1975, Needham et al. 2000).

Presented here are the actual states of diagnostic characters observed in large series of *T. lacerata* and *T. onusta* specimens. These data were used to analyze the efficacy of previously published characterizations in distinguishing between the two species. The most reliable characteristics we found to distinguish *T. lacerata* from *T. onusta* are presented.

MATERIALS AND METHODS

A total of 35 specimens of exuviae or final instars were used in this analysis, all collected from ponds in the Prairie Region of Missouri. Specifically, exuviae of 20 *T. onusta* and 2 *T. lacerata* reared by BHPL were used in this analysis, as were two final instars of *T. lacerata* that were collected with and obviously conspecific to the reared *T. lacerata* specimens and died shortly before emergence. Exuviae of seven reared *T. lacerata* and four reared *T. onusta* from the reference collection of Grabau (1955) also were used. The head of one specimen of *T. lacerata* was damaged and not measured and the epiproct of one *T. onusta* was deformed and not included in analyses involving this character. All specimens are housed at the Enns Entomology Museum, University of Missouri-Columbia.

Measurements were performed under magnification using an ocular micrometer. Cerci and epiprocts were measured in strict dorsal view from the posterodorsal margin of abdominal segment X. Paraprocts were measured in strict ventral view from the posteroventral margin of segment X. Lateral spines were measured in strict dorsal view from the posterior margin of the abdominal tergum immediately adjacent to their base. Although paired, only one paraproct, one cercus, and both spines of one side were measured per specimen. Antennae often required removal to arrange in two dimensions for accurate measurement. For consistency, the right was removed and measured unless it had been lost. Because of distortion during emergence, head width was measured in strict dorsal view from the most lateral point of the compound eye to the coronal suture and multiplied by two.

When assigning a character with a continuous distribution to one of two discrete groups, a limiting value must be established. For *T. lacerata* and *T. onusta*, we used the mean of each pair of published distinguishing character states. Thus, the secerning value is 0.75 when evaluating if the cerci are ≤ 0.7 times or ≥ 0.8 times the length of the epiproct, and 0.85 when evaluating if the cerci are ≤ 0.8 times or ≥ 0.9 times the length of the epiproct. The secerning value of the two given antennal states is 0.58, and that of the given states of the lateral spines is 0.9.

Material examined.— MISSOURI: AUDRAIN CO.: Robert M. White II Conservation Area, 29 August and 3 September 2000, UTM X 597100, UTM Y 4353150, BHPL (exuviae of 20 reared *T. onusta*); BOONE CO.: University of Missouri South Farms, 16 August 2000, UTM X 562100, UTM Y 4306350, BHPL (2 larval *T. lacerata*, exuviae of 2 reared *T. lacerata*); 2.5 mi. W of Ashland, 14 August – 18 September 1953, M. C. Grabau (exuviae of 3 reared *T. lacerata*, exuviae of 3 reared *T. onusta*); pond, Columbia, 15 and 18 June 1953, M. C. Grabau (exuviae of 2 reared *T. lacerata*); pond, Columbia, 26 August 1953, M. C. Grabau (exuviae of 1 reared *T. onusta*); pond, 16 September 1953, M. C. Grabau (exuviae of 1 reared *T. lacerata*); 3 September 1953, M. C. Grabau (exuviae of 1 reared *T. lacerata*).

RESULTS

The mean length of all characters measured except antennal segments was greater in *T. lacerata* (Table 1). Of the characters measured, only epiproct length showed no overlap between the two species.

Considerable overlap between the species was found in cerci length to epiproct length ratios (Fig. 1). The character states of cerci ≤ 0.7 times versus ≥ 0.8 times the length of the epiproct correctly identified 9% of *T. lacerata* larvae and 100% of *T. onusta* larvae. Alternatively, the character states of cerci 0.8 times versus 0.9 times the length of the epiproct correctly identified 91% of *T. lacerata* specimens and 57% of *T. onusta* specimens.

The relative length of antennal segments three and four showed extensive overlap between species (Table 2), but much of this overlap was due to an aberrant specimen of each species. The character state of antennal segment four 0.5 times the length of three in *T. lacerata* and 0.67 times in *T. onusta* correctly identified 73% of *T. lacerata* specimens and 84% of *T. onusta* specimens.

The relative lengths of the lateral spines of abdominal segments VIII and IX exhibited very little overlap (Fig. 2). The largest value seen in the *T. lacerata* specimens (0.86) was equal to the smallest value seen in those of *T. onusta*. This character state correctly identified 100% of *T. lacerata* specimens and 71% of *T. onusta* specimens. If the secerning value for *T. lacerata* was established at 0.86, 100% of *T. lacerata* specimens and 88% of *T. onusta* specimens would be correctly identified.

The ratio of epiproct length to paraproct length showed no overlap between specimens of *T. lacerata* and *T. onusta* (Fig. 3). In *T. lacerata*, the epiproct

Table 1. Measurements (mm) of morphological characters of specimens of *Tramea lacerata* and *T. onusta*. Italicized values overlap between species. All specimens were exuviae except two final larval instar *T. lacerata* (indicated by *).

Species/ specimen	**Cercus**	**Epiproct**	**Paraproct**	**Third antennal segment**	**Fourth antennal segment**	**Head width**	**Spine of 8**	**Spine of 9**
T. lacerata 1	2.40	2.96	2.88	*0.80*	*0.49*	7.51	2.80	3.40
2	*2.16*	2.60	*2.73*	0.63	*0.53*	*7.27*	*2.40*	3.20
3	2.40	2.76	2.92	*0.78*	*0.41*	*7.27*	2.68	3.16
4	2.28	2.84	2.96	*0.80*	*0.41*	7.51	*2.48*	3.20
5	2.32	2.78	*2.76*	*0.82*	*0.47*	N/A	*2.42*	3.00
6	*2.12*	2.64	*2.72*	*0.72*	*0.49*	*7.04*	*2.40*	*2.80*
7	*2.16*	2.68	*2.68*	*0.78*	*0.45*	*6.96*	*2.24*	3.12
8*	2.24	3.12	3.00	*0.88*	*0.49*	7.75	2.72	3.40
9*	2.40	2.96	2.98	0.98	*0.55*	7.90	*2.60*	3.04
10	*2.16*	2.72	*2.68*	*0.82*	*0.47*	*7.22*	*2.56*	3.16
11	*2.12*	2.52	*2.56*	*0.80*	*0.43*	*7.04*	*2.20*	*2.56*
mean	**2.25**	**2.78**	**2.81**	**0.80**	**0.47**	**7.35**	**2.50**	**3.09**
s.e.	**0.11**	**0.18**	**0.15**	**0.08**	**0.04**	**0.32**	**0.19**	**0.25**

Table 1. Continued.

Species/ specimen	Cercus	Epiproct	Paraproct	Third antennal segment	Fourth antennal segment	Head width	Spine of 8	Spine of 9
T. onusta 1	1.80	2.08	2.28	*0.68*	*0.43*	6.80	2.04	2.20
2	1.72	2.08	*2.56*	*0.66*	*0.43*	6.88	2.08	2.32
3	1.92	2.04	2.24	*0.74*	*0.45*	6.72	1.96	2.08
4	1.88	2.12	2.44	*0.78*	*0.49*	*6.96*	*2.48*	2.44
5	1.80	2.28	*2.56*	*0.82*	*0.53*	*7.11*	2.04	2.38
6	1.96	2.04	2.28	*0.82*	*0.53*	6.88	2.12	2.28
7	1.76	2.04	2.40	*0.80*	*0.45*	6.72	*2.32*	2.44
8	1.68	N/A	2.40	*0.78*	*0.51*	*7.04*	2.16	2.36
9	*2.16*	2.24	*2.72*	*0.80*	*0.49*	*6.96*	*2.50*	*2.68*
10	2.00	2.48	*2.84*	*0.82*	0.60	6.72	*2.48*	*2.88*
11	1.86	2.24	*2.60*	*0.86*	*0.51*	6.88	*2.24*	2.52
12	2.04	2.20	2.48	*0.92*	*0.51*	*6.96*	*2.22*	2.48
13	1.88	2.20	*2.60*	*0.88*	*0.51*	*6.96*	*2.28*	2.40
14	1.68	2.12	2.40	*0.78*	*0.51*	*6.96*	2.04	2.38
15	1.84	2.22	2.52	*0.78*	*0.47*	6.88	*2.28*	2.48
16	1.96	2.32	*2.76*	*0.91*	*0.55*	*7.38*	*2.44*	*2.64*
17	2.00	2.28	*2.68*	*0.84*	*0.49*	6.72	*2.40*	*2.64*
18	1.92	2.12	2.48	*0.72*	0.29	6.72	2.04	2.32
19	1.72	2.04	*2.56*	*0.88*	*0.53*	*7.27*	*2.60*	*2.72*
20	2.08	2.36	*2.64*	*0.82*	*0.53*	*7.27*	*2.32*	*2.64*
21	1.72	2.08	2.32	*0.84*	*0.55*	*7.14*	2.12	2.36
22	2.00	2.16	2.52	*0.84*	*0.49*	*7.11*	*2.28*	2.40
23	1.88	2.32	*2.62*	*0.84*	*0.51*	*7.11*	*2.44*	*2.74*
24	1.94	2.04	2.46	*0.78*	*0.49*	6.80	2.12	2.28
mean	**1.88**	**2.18**	**2.51**	**0.81**	**0.49**	**6.96**	**2.25**	**2.46**
s.e.	**0.13**	**0.12**	**0.16**	**0.06**	**0.06**	**0.19**	**0.18**	**0.19**

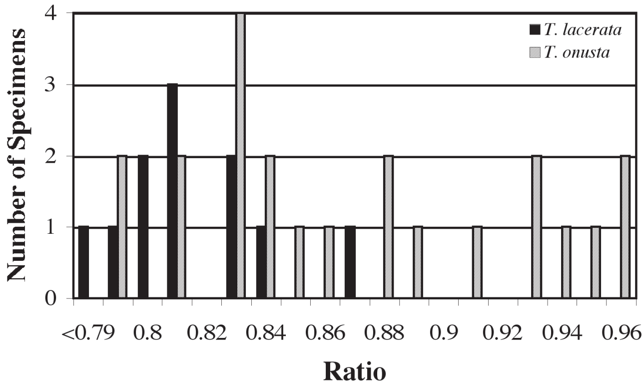

Figure 1. Frequency of cercus/epiproct length ratios expressed by larval *Tramea*.

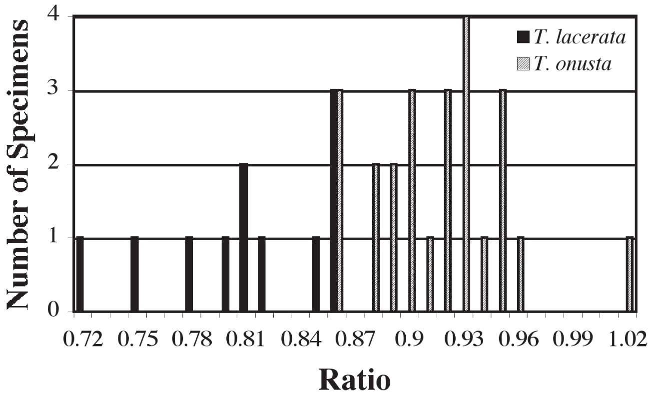

Figure 2. Frequency of spine 8/spine 9 length ratios expressed by larval *Tramea*.

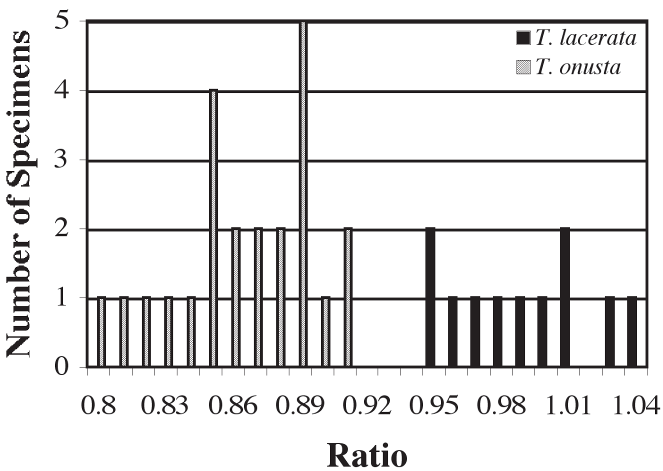

Figure 3. Frequency of epiproct/paraproct length ratios expressed by larval *Tramea*.

Table 2. Character length ratios of specimens of *Tramea lacerata* and *T. onusta*. Italicized values overlap between species. All specimens were exuviae except two final larval instar *T. lacerata* (indicated by *).

Species/ specimen	Cercus/ epiproct	Epiproct/ paraproct	Cercus/ paraproct	Antennal segment 4/ antennal segment 3	Spine of 8/ spine of 9
T. lacerata 1	*0.81*	1.03	*0.83*	*0.61*	0.82
2	*0.83*	0.95	*0.79*	0.83	0.75
3	*0.87*	0.95	*0.82*	*0.53*	0.85
4	*0.80*	0.96	*0.77*	*0.51*	0.78
5	*0.83*	1.01	*0.84*	*0.57*	0.81
6	*0.80*	0.97	*0.78*	*0.68*	*0.86*
7	*0.81*	1.00	*0.81*	*0.58*	0.72
8*	0.72	1.04	*0.75*	*0.56*	0.80
9*	*0.81*	0.99	*0.81*	*0.56*	*0.86*
10	*0.79*	1.01	*0.81*	*0.57*	0.81
11	*0.84*	0.98	*0.83*	*0.54*	*0.86*
mean	**0.81**	**0.99**	**0.80**	**0.59**	**0.81**
s.e.	**0.04**	**0.03**	**0.03**	**0.09**	**0.05**
T. onusta 1	*0.87*	0.91	*0.79*	*0.63*	0.93
2	*0.83*	0.81	0.67	*0.65*	0.90
3	0.94	0.91	*0.86*	*0.61*	0.94
4	0.89	0.87	*0.77*	*0.63*	1.02
5	*0.79*	0.89	0.70	*0.64*	*0.86*
6	0.96	0.89	*0.86*	*0.64*	0.93
7	*0.86*	0.85	0.73	*0.56*	0.95
8	N/A	N/A	0.70	*0.65*	0.92
9	0.96	0.82	*0.79*	*0.61*	0.93
10	*0.81*	0.87	0.70	*0.74*	*0.86*
11	*0.83*	0.86	0.72	*0.59*	0.89
12	0.93	0.89	*0.82*	*0.55*	0.90
13	*0.85*	0.85	0.72	*0.58*	0.95
14	*0.79*	0.88	0.70	*0.65*	*0.86*
15	*0.83*	0.88	0.73	*0.60*	0.92
16	*0.84*	0.84	0.71	*0.60*	0.92
17	0.88	0.85	*0.75*	*0.58*	0.91
18	0.91	0.85	*0.77*	0.41	0.88
19	*0.84*	0.80	0.67	*0.60*	0.96
20	0.88	0.89	*0.79*	*0.64*	0.88
21	*0.83*	0.90	0.74	*0.65*	0.90
22	0.93	0.86	*0.79*	*0.58*	0.95
23	*0.81*	0.89	0.72	*0.60*	0.89
24	0.95	0.83	*0.79*	*0.63*	0.93
mean	**0.87**	**0.87**	**0.75**	**0.61**	**0.91**
s.e.	**0.05**	**0.03**	**0.05**	**0.06**	**0.04**

was longer than the paraprocts in 36% of the specimens, with the mean ratio 0.99. In all *T. onusta*, the epiproct was shorter than the paraprocts. The minimum ratio of epiproct length to paraproct length in *T. lacerata* specimens was 0.95, and the maximum value in *T. onusta* was 0.91.

DISCUSSION

The results demonstrate that none of the published key character states is 100% reliable in distinguishing larval specimens of *T. lacerata* from *T. onusta* in the Prairie Region of Missouri. Of the published characters, the ratio of length of the lateral spines of abdominal segment VIII to those of IX was the most reliable. However, the ratio of epiproct length to paraproct length holds promise as a diagnostic character distinguishing *T. lacerata* from *T. onusta*, although more specimens from a broader geographic range should be examined. Further, our observations agree with those of Bick (1951) that the lateral spines, epiprocts, and paraprocts are less ontogenetically mutable than are cerci or antennal segments.

The results strongly suggest that the key character state of epiproct longer than paraprocts should not be used to characterize either of these species of *Tramea*, especially *T. onusta*. We have examined numerous specimens of *Tramea* collected from Missouri and reared *Tramea* at the FSCA and Snow Museum, and in no specimen did the tip of the epiproct attain the level of the tips of the paraprocts. If all caudal appendages were measured in dorsal aspect from the posterodorsal margin of abdominal segment X, the epiproct would invariably measure shorter than the paraprocts. This is because abdominal segment X is longer ventrally than dorsally, which illustrates the necessity to clearly indicate from which aspect the character was measured.

Much of the confusion concerning the relative lengths of the caudal appendages can be traced to several errors by Byers (1927). The measurements given in his larval description of *T. onusta* were consistent with the ratios presented in couplet three of his key to species and are corroborated by the results of the present study. However, the ratios he gave in the description and in couplet two are contradictory to his measurements, couplet three of his key to species, the results of the present study, and to themselves. However, it is the aberrant ratios of Byers that Irinue de Souza et al. (1999) apparently incorporated into their key to species. Klots (1932) also adopted the key and diagnosis of Byers, distinguishing *T. onusta* as possessing cerci longer than epiproct in her key, but diagnosed the species as possessing cerci 0.67 times as long as the epiproct. This may also account for the discrepancies between the taxonomic keys and diagnoses of Walker and Corbet (1975).

The ratios given by Byers (1927) in his diagnosis are consistent with his absolute measurements if the words "dorsal" and "inferior" are transposed in line three of p. 73. Further, if the word "shorter" is replaced with "longer" in line three of couplet two in his key to species, the key is transformed from highly contradictory to reasonably accurate. In fact, Byers (1930) made the latter amendment in his key to species, but retained the erroneous ratios in his diagnosis.

The search for reliable larval characters to distinguish species of *Tramea* has generated considerable confusion in the literature. Regrettably, this study suffers from two of the same restrictions undoubtedly responsible for some of this confusion: too few specimens and too limited a geographic area. Therefore, this study does not aim to conclusively settle the matter, but has three less lofty goals. The first is to provide data concerning key character states of these species of *Tramea*. The second is to caution researchers conducting ecological, behavioral, or distributional studies involving larval Odonata to be very careful when performing species level determinations of *Tramea*. Finally, it is hoped that this will encourage odonatologists from other regions to closely examine their larval specimens of *Tramea*. Then we will be able to begin to identify, and quantify the variability of, potentially distinguishing characteristics rather than continue to perpetuate those we know to be unreliable.

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