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How Did E. M. Walker Measure the Length of the Labium of Nymphs of *Aeshna* and *Rhionaeschna* (Odonata: Aeshnidae)?

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Abstract

The exhaustive studies of nymphs of *Aeshna* Fabricius and *Rhionaeschna* Förster by E. M. Walker (1912-1958) have long guided the taxonomy of these groups and formed the basis for keys still in use today. However, uncertainty about how he measured the length of the labium, including the varied terminology he used over the duration of his career concerning this structure, has led to confusion about application of his taxonomic recommendations. We recalculated ratios of the maximum width/length [W(max)/L] by measuring the illustration dimensions of folded labia and prementums in publications throughout his career and compared these data with the ratios he stated in those publications and with ratios derived from measurements of specimens in our collections. Our results show that from 1912 to 1941, Walker restricted length measurement to the prementum proper (which he called the "mentum of the labium"), exclusive of the ventrally visible portion of the postmental hinge. However, in 1941 he reported ratios from length measurements done two ways, excluding the postmental hinge in his description of the nymph of *A. verticalis* Hagen, but including the hinge in his description of the nymph of *A. septentrionalis* Burmeister (Whitehouse 1941). In Walker's most recent and influential work (1958), he included the postmental hinge in labium length measurements of nine species, but restricted length measurements to the prementum for five others. He was consistent with the use of terms, using both "folded labium" by which he meant the prementum plus the postmental hinge, and "prementum" by which he meant only that structure. However, Walker's descriptions of the labium in his latest work are buried in long, frequently punctuated sentences that for most species include the terms "folded labium" and "prementum" in the same sentence, so careful reading is required to know which term is intended in the width/length ratio. Width/length ratios we each calculated independently were invariably similar for a given species and were usually similar to Walker's stated ratio for that species. These similarities affirm our conclusion that while labium measurements must be done with care, they are closely repeatable among workers and will consistently lead to correct determinations in properly designed couplets of dichotomous keys to these genera. We recommend measuring the length of the prementum proper in future studies of these genera when labium ratios are calculated because we found less variability in those cases than when the measurements included the postmental hinge. An approximate conversion between the two methods of calculating W(max)/L ratios can be made as follows: ratio calculated when the length of the prementum excluding the postmental hinge is used x 0.88 is approximately equal to the ratio when the postmental hinge is included for species of *Aeshna* and *Rhionaeschna* in North America.

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The shape of the ventrally visible portion of the labium is a valuable distinguishing characteristic for nymphs of a number of species of *Aeshna* Fabricius and *Rhionaeschna* Förster in North America. The famous Canadian entomologist E. M. Walker undertook exhaustive studies of the nymphs of *Aeshna*, including the recently assigned genus *Rhionaeschna* (von Ellenrieder 2003), in which he typically illustrated the labium and at various times measured its greatest width, distal width, basal width, and length. These illustrations included the labial palps, movable hooks, prementum, and the distal, ventrally visible portion of the postmentum (often called the postmental hinge). From measurements of the labium Walker calculated ratios which he often presented in diagnoses and included in dichotomous keys to species within the genus *Aeshna*. He published the illustrations and ratios in numerous works including a detailed monograph of the genus (Walker 1912), in Volume 2 of his seminal work on the Odonata of Canada and Alaska (Walker 1958), and in a number of smaller papers (Walker 1922, 1934, 1941; Whitehouse 1941).

Unfortunately, he did not, to our knowledge, specifically describe how the length of the labium was measured in any of these works. In looking at this structure in ventral view, there are two primary ways that its length might be measured. Measurements could be limited to the prementum proper (not including the labial palps, movable hooks, or the postmental hinge), because it is the primary structure of the labium. Alternatively, the ventrally visible portion of the postmental hinge could be included in length measurements with the prementum (hereafter "folded labium") because it bends back upon itself to hold the prementum close to the underside of the head when not extended, and is therefore clearly visible in ventral view (Fig. 1). Substantially different maximum width/length [W(max)/L] ratios would result depending on which length measurement was used.

While trying to reconcile our ratios of labial W(max)/L for a number of species of North American *Aeshna* and *Rhionaeschna* with Walker's ratios, it was not always apparent how he had measured the length of the labium. In his most recent publication (Walker 1958) he appeared to have included the postmental hinge in most, but not all, of his measurements, and in other earlier works, he apparently measured only the prementum. Further, over the course of his lengthy career, Walker used a variety of descriptive terms for aspects of the ventrally visible portion of the labium including folded labium, labium, mentum of the labium, and prementum when describing length and width dimensions of that mouth part. This uncertainty about how he measured the length of the labium led to some confusion about our determinations of *Aeshna* and *Rhionaeschna* nymphs when using his key (Walker 1958). Elements of Walker's key to the genus *Aeshna* have formed the basis upon which recent North American keys to *Aeshna* and *Rhionaeschna* were built. Our objective was to determine how Walker measured the length of the labia of *Aeshna* and *Rhionaeschna* nymphs in his studies. We approached this objective by comparing the width/length ratios of folded labia or prementums of nymphs of *Aeshna* and *Rhionaeschna* as stated by Walker in his publications, with ratios that we calculated from measurements of his illustrations, and with similarly derived ratios from measurements of specimens in our collections.

Materials and Methods

We examined ratios of prementum and folded labium maximum width/length [W(max)/L] for the 16 species of *Aeshna* and *Rhionaeschna* that Walker illustrated in his publications. We compared ratios that we calculated from measurements of his illustrations of labia, both with and without the postmental hinge, with his stated ratios for those species in the same publications, and with similarly derived ratios from measured specimens in our collections. Measurements were made from illustrations in Walker's publications with

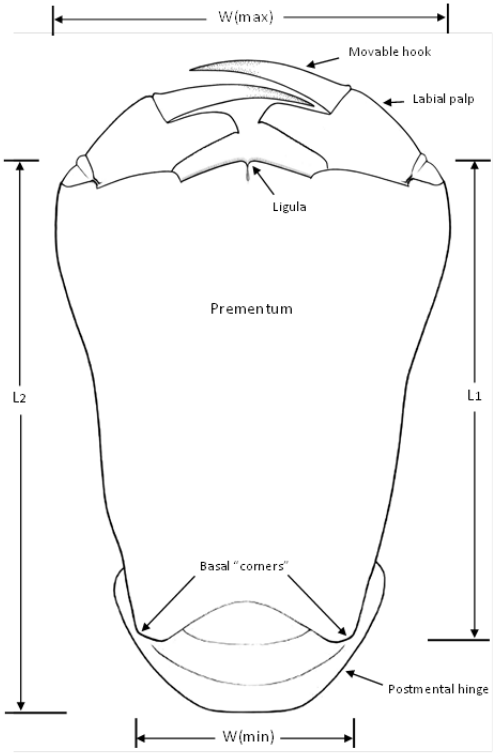

Figure 1. Folded labium of *Aeshna canadensis* (F-0 nymph) in ventral view showing how we measured the maximum or greatest width of the prementum [W(max)], minimum or basal width of the prementum [W(min)], length of the prementum (L1), and length of the folded labium including the postmental hinge (L2).

a millimeter rule to the nearest 0.05mm. We consider this to be a valid data collection technique because Walker presumably drew his illustrations with a camera lucida and they should therefore reflect the actual proportions of the folded labia of the specimens drawn. Maximum width was measured where it occurred in the distal 2/3rds of the prementum (Fig. 1). Length of the prementum was measured along the midline from the distal or anterior margin of the prementum (ligula) to a straight line envisioned between the angular "corners" at the base (Fig. 1, measurement "L1", exclusive of the postmental hinge). We also measured the folded labium length including the postmental hinge (Fig. 1, measurement "L2"). In most cases Walker had illustrated the folded labium of a species more than once, so all of the illustrations of a species were measured, and we noted if there were substantial differences in ratios derived among them. Our analyses consisted of simple comparisons to determine for each species which of the calculated ratios -- when the postmental hinge was included in the length measurement, and when it was not -- was closer to Walker's stated ratio in the same publication. We also noted the terminology he used for the labia he illustrated in publications throughout his career.

Ratios [W(max)/L] were similarly calculated from measurements of exuviae and F-0 nymphs from our collections made in ventral view under magnification with an ocular micrometer (to the nearest 0.05 mm). We preferred to use reared

(= associated) exuviae to be certain of their identity. When rearing, nymphs were collected after molting to the final instar (F-0) and were reared to emergence in indoor aquaria. In some cases, associations in the process of emerging were collected in the field – in these cases they were placed in small live cages while still on their emergence supports and were allowed to complete the emergence process. Exuviae were placed in individual vials of 70% ethanol. Teneral adults were maintained alive in cages for several days after emergence, then were either placed in the vial of alcohol with their exuvia or were soaked overnight in acetone, dried, and stored in standard Odonata envelopes. If the teneral/exuvia association was stored separately, each was given a unique accession number immediately after emergence to preclude any possibility of confusing the specimens. However, our sample sizes of reared exuviae were fewer than 10 for most species, so in those cases we augmented the sample with unassociated exuviae or F-0 nymphs to achieve a sample size of 10 for all species (Table 1). In all cases where this augmentation was done we ensured that the nymphs and exuviae were firmly determined based on the following criteria: 1) were identifiable using current keys, 2) were similar to the reared specimens for that species, and 3) were from sites where the species was common and similar appearing species were not expected. *Aeshna clepsydra* and *A. constricta* were not reared, but their nymphs are distinctive and most specimens were selected from sites where each was the dominant species of *Aeshna*. All specimens were determined and measured by the authors and are housed in the Odonata Collection of the Wisconsin Department of Natural Resources in Superior and in the personal collection of KJT in Wautoma, Wisconsin.

Results and Discussion

During his career, E. M. Walker described the dimensions and published illustrations of the folded labia of 16 species of North American *Aeshna* and *Rhionaeschna*. Among these, he described the place on the labium where he measured the width, named the structure for which he calculated a width/length ratio, and stated the ratio for 13 species. For *A. subarctica, R. californica*, and *R. mutata* he did not provide a ratio. He stated that the labium of *A. subarctica* was "indistinguishable from that of *A. juncea*" (Walker 1912) and that the head and eyes were "as in *juncea*" (Walker 1958). For *R. californica* he simply stated that the distal width was "a little less than the length" of the prementum (Walker 1912, 1958). Of *R. mutata* he noted that the nymph was "very like that of *A. multicolor*, all parts of the head apparently indistinguishable in the two species" (Walker 1958).

Walker illustrated most species of North American *Aeshna* and *Rhionaeschna* twice. That these were different illustrations of the same species, and not just modified versions of the same drawing, is demonstrated by differences between them in stippling, shape contours, and positioning of the movable hooks. He illustrated North American specimens of *A. juncea* three times (Walker 1912, 1934, and 1958; he also illustrated Eurasian specimens of *A. juncea*). Species he illustrated only once were *A. tuberculifera* and *R. mutata*, both published in 1958. Although our measurements of his illustrations gave similar width/length ratios for most species between and among time periods, there were some notable exceptions. For example, in comparing our calculated W(max)/L ratios of the folded labia (including the postmental hinge) of his illustrations between 1912 and 1958 we note differences of 0.64 vs. 0.70 for *A. canadensis*, 0.66 vs. 0.71 for *A. interrupta*, 0.67 vs. 0.76 for *A. juncea* (quite a substantial difference), 0.59 vs. 0.64 for *A. septentrionalis*, and 0.79 vs. 0.86 for *R. californica*. Because Walker's illustrations were evidently done with a camera lucida, they should reflect the actual proportions of the labia drawn. Thus these differences in his illustrations of a species between time periods could be due to intraspecific morphological variation, to some unidentified source of methodological error, or a combination of the two.

Table 1. Sampling locations and sample sizes (n) for 16 species of *Aeshna* and *Rhionaeschna* for which prementum dimensions were measured (reared exuviae = re; unassociated exuviae = un; F-0 nymph = ny).

Species	**Locality and sample size**
Aeshna canadensis Walker	1. MN, Carlton Co., bog pond, Gandy Dancer Trail (*n* = 1 re) 2. WI, Ashland Co., lagoon, Michigan Island (*n* = 2 re) 3. WI, Ashland Co., Bark Bay, Lake Superior (*n* = 2 un) 4. WI, Douglas Co., Balsam Cr., Foxboro-Chaffey Rd. (*n* = 3 re) 5. WI, Douglas Co., Breitzman Lake (*n* = 1 re) 6. WI, Douglas Co., Mulligan Lake (*n* = 1 re)
Aeshna clepsydra Say	1. MA, Barnstable Co., Snow Pond, Truro (*n* = 1 un, 2 ny) 2. NY, Rensselaer Co., White Lily Pond, Grafton (*n* = 5 un) 3. WI, Douglas Co., Apple Lake (*n* = 1 un) 4. WI, Douglas Co., Bird Sanctuary Pond, Gordon (*n* = 1 un)
Aeshna constricta Say	1. WI, Door Co., North Bay (*n* = 2 un) 2. WI, Door Co., Mink River (*n* = 4 un) 3. WI, Douglas Co., Allouez Bay, Lake Superior (*n* = 2 un) 4. WI, Douglas Co., Little Pokegama Bay, St. Louis River (*n* = 1 un) 5. WI, Douglas Co., shoreline panne, Lake Superior, Brule River State Forest (*n* = 1 un)
Aeshna eremita Scudder	1. ON, Amikeus Lake, Algonquin Provincial Park (*n* = 1 un) 2. MN, Lake Co., Kangas Lake (*n* = 3 re) 3. WI, Ashland Co., Dry Lake (*n* = 1 un) 4. WI, Ashland Co., Lake Three (*n* = 1 un) 5. WI, Bayfield Co., unnamed pond, Koski Rd. (*n* = 1 un) 6. WI, Douglas Co., Mulligan Lake (*n* = 2 un) 7. WI, Douglas Co., Pond A, Kimmes-Tobin Wetland (*n* = 1 un)
Aeshna interrupta Walker	1. ND, Grand Forks Co., Marsh Pond, Turtle River State Park (*n* = 6 re) 2. WI, Douglas Co., pond, Vapa Rd., Brule River State Forest (*n* = 4 re)
Aeshna juncea (Linnaeus)	1. ON, Algoma Dist., Lake Superior, Schreiber Channel nr. Nicol Island (*n* = 1 re) 2. AK, Bethel Co., pond nr. Bethel Airport (*n* = 1 re, 3 un, 1 ny) 3. AK, Bethel Co., pond nr. Tundra Ridge Road, Bethel (*n* = 1 ny) 4. CO, Gunnison Co., Iron Fen, Crested Butte (*n* = 1 un) 5. OR, Marion Co., pond, NF-6370, Willamette National Forest (*n* = 1 re) 6. WA, Skamania Co., Olallie Lake, NR-5601, Gifford Pinchot National Forest (*n* =1 re)
Aeshna palmata Hagen	1. CA, Mono Co., pond nr. Tioga Road, Yosemite National Park (*n* = 1 re) 2. OR, Deschutes Co., Todd Lake (*n* = 9 un)
Aeshna septentrionalis Burmeister	1. BC: pond nr. Skagway Rd. (*n* = 1 un) 2. YT, fen nr. Blackstone River & Dempster Hwy (*n* = 1 ny) 3. YT, fen nr. Eagle River & Dempster Hwy (*n* = 2 ny) 4. YT, fen, Koidern (*n* = 1 ny) 5. YT, fen nr. Long's Creek & Alaska Hwy (*n* = 1 ny) 6. YT, fen nr. Nahanni Range Rd. (*n* = 1 un) 7. YT, fen, North McMillan River Valley, (*n* = 2 ny) 8. YT, fen nr. Slims River & Alaska Hwy (*n* = 1 re)

Table 1. Continued.

Species	Locality and sample size
Aeshna sitchensis Hagen	1. MI, Alger Co., fen nr. Masters (*n* = 1 ny) 2. MN, Carlton Co., fen NE of Whyte (*n* = 1 re, 4 ny) 3. WI, Ashland Co., fen, Stockton Island (*n* = 4 un)
Aeshna subarctica Walker	1. SK, fen, Hwy SK 2 (*n* = 1 re) 2. ME, Somerset Co., Twelve Mile Bog (*n* = 1 re) 3. WI, Douglas Co., Breitzman Lake (*n* = 1 un) 4. WI, Iron Co., bog pond nr. Tyler Forks (*n* = 1 re, 6 un)
Aeshna tuberculifera Walker	1. MN, Washington Co., pond, Warner Nature Center (*n* = 4 re) 2. WI, Ashland Co., lagoon, Michigan Island (*n* = 1 un) 3. WI, Douglas Co., pond, Hwy 2, Brule River State Forest (*n* = 2 re, 2 ny) 4. WI, Douglas Co., pond, Vapa Road, Brule River State Forest (*n* = 1 un)
Aeshna umbrosa Walker	1. MA, Berkshire Co., tributary of Laurel Lake (*n* = 2 re) 2. MN, Becker Co., Ottertail River, Tamarac National Wildlife Refuge (*n* = 3 re) 3. WI, Bayfield Co., Flag River (*n* = 1 re) 4. WI, Burnett Co., Kleiss Pond, Grantsburg (*n* = 1 re) 5. WI, Douglas Co., Balsam Creek, Foxboro-Chaffey Rd. (*n* = 1 re) 6. WI, Douglas Co., Breitzman Lake (*n* = 1 re) 7. WI, Washburn Co., Little MacKay Creek (*n* = 1 re)
Aeshna verticalis Hagen	1. MI, Alger Co., fen nr. Masters (*n* = 1 re, 1 ny) 2. WI, Bayfield Co., bog, Quarry Rd., Port Wing (*n* = 1 un) 3. WI, Douglas Co., bog, Empire Wilderness Area (*n* = 1 un) 4. WI, Green Lake Co., White River Marsh (*n* = 1 re, 2 ny) 5. WI, Iowa Co., Wisconsin River slough, Muscoda (*n* = 1 re, 2 ny)
Rhionaeschna californica (Calvert)	1. CA, Tuolumne Co., Birch Lake (*n* = 1 ny) 2. OR, Benton Co., pond, Corvallis (*n* = 1 ny) 3. OR, Hood River Co., pond nr. Columbia River Hwy, Mt. Hood National Forest (*n* = 4 ny) 4. UT, Tooele Co., pond, Timpie Springs Waterfowl Management Area (*n* = 2 ny) 5. WA, Spokane Co., Blackhorse Lake, Turnbull National Wildlife Refuge (*n* = 1 re) 6. WA, Spokane Co., Kepple Lake, Turnbull National Wildlife Refuge (*n* = 1 re)
Rhionaeschna multicolor (Hagen)	1. CA, Inyo Co., pond nr. 5 Bridges Road (*n* = 1 re) 2. CA, San Mateo Co., Searsville Lake, Jasper Ridge Biological Preserve (*n* = 1 re) 3. OR, Lane Co., pond, Pirtle Rd. (*n* = 3 un) 4. WI, Eau Claire Co., retention pond, Eau Claire (*n* = 3 re, 2 un)
Rhionaeschna mutata (Hagen)	1. MN, Washington Co., pond, Warner Nature Center (*n* = 1 re, 1 un) 2. WI, Marquette Co., Stoicks Pond (*n* = 4 un) 3. WI, Walworth Co., pond, Kettle Moraine State Forest, So. Unit (*n* = 2 ny) 4. WI, Waukesha Co., pond, Kettle Moraine State Forest, So. Unit (*n* = 2 ny)

During the course of his career Walker used different terms for wide part of the labium he measured and clearly intended specific meanings by use of these terms. For some species Walker measured the maximum width of the prementum, which he referred to as the greatest width or greatest breadth, but for other species he measured the distal width, which he often called apical width or apical breadth. Distal width and greatest width are not equivalent and do not necessarily give similar width/length ratios for all species because the greatest width may be some distance from the distal-most part of the prementum. For some species Walker explicitly stated that the folded labium was widest at the distal end of the prementum, and for others, that the greatest width was some distance before the distal end.

In his earliest work, Walker (1912) consistently referred to the illustrated structure as the "mentum of the labium," of which he usually measured the apical (= distal) breadth. He stated a width/length ratio for nine species in this publication. When we compared ratios we derived from his illustrations for these species with his stated ratios, we found that all but one had stated ratios that were closer to the illustration ratio without the postmental hinge than to the illustration ratio with the hinge included (Table 2). The single exception, *A. juncea*, had a stated ratio of "the apical breadth a little more than 2/3rds of the length," which is ambiguous when compared with calculated illustration ratios that are both 2/3rds or greater. We therefore conclude that early in his career Walker measured the prementum proper, without including the postmental hinge. Walker (1912) did not illustrate the folded labium of *A. subarctica*, stating only that it was indistinguishable from that of *A. juncea*.

In his works published from 1922 through 1941 Walker continued to describe the structure as the mentum of the labium and by that continued to mean, in most cases, just the prementum proper exclusive of the postmental hinge. Thus, his 1922 description of the nymph of *A. sitchensis* does not include the postmental hinge in his stated ratio of about 0.80 (Table 2). In 1934 Walker gave no mention of making any labial length measurements of either *A. juncea* or *A. subarctica*. We therefore lack any basis for making a judgment about how he interpreted the length of the structure at that time. In his 1941 description of the nymph of *A. verticalis*, Walker stated that the greatest width of the mentum of the labium was 3/4ths of the length, which is again fully consistent with the postmental hinge being excluded from measurement (Table 2). In this paper, Walker (1941) also stated that the distal widths of the labia were 80% to 85% of the length for both *A. juncea* and *A. subarctica,* which is consistent with the postmental hinge being excluded in the labial length measurements of both species. However, Walker's measurement of the length of the mentum of the labium in his description of the nymph of *A. septentrionalis* in the same year (Whitehouse 1941) is noteworthy because for the first time his stated ratio of "greatest breadth three-fifths of length" evidently included the postmental hinge (Table 2).

In his most recent work (1958), Walker's treatment of the labium was inconsistent among the 16 species, requiring careful reading to ascertain the intended meaning of the individual elements. His descriptions of the labium from this work are excerpted in Table 3, where it is evident that his descriptions of the labium are often buried in long, frequently punctuated sentences that for most species include the terms "folded labium" and "prementum" in the same sentence. Therefore, careful attention is required to know which length measurement is intended in the width/length ratio. Walker (1958) referred to the following aspects or ratios involving the labium, though not all of them for each species and not always in the same order (number of species for which that aspect or ratio was referred to in parentheses): how far back the folded labium reached relative to the position of the mesocoxae (7) or hind coxae (1); where the folded labium was widest (6); the greatest or distal width/length ratio for the folded labium (9) or the prementum (5); the ratio of the width of the

Table 2. Labium ratios (width/length) of exuviae or F-0 nymphs of 14 species of *Aeshna* and *Rhionaeschna* as stated by Walker from 1912 through 1941 and as we calculated from measurements of his illustrations for those years (with and without the postmental hinge). Underlined ratios (where applicable) are the closer of the pair of ratios from Walker's illustrations to his stated ratio. Labium width is either apical [= distal] or maximum [= greatest], with the terms he used for each species given in rightmost column.

Species	Walker's stated ratios	Ratios calculated from measurements of Walker's illustrations		Walker's terms for the distal or maximum width of the labia he measured
		without hinge	with hinge	
A. canadensis[a]	>0.71	0.72	0.64	apical breadth
A. clepsydra[a]	0.71	0.73	0.64	apical breadth
A. constricta[a]	~0.86	0.88	0.76	apical breadth
A. eremita[a]	~0.78	0.81	0.70	apical breadth
A. interrupta[a]	~0.71	0.75	0.66	apical breadth
A. juncea[a]	≥0.67	0.74	0.67	apical breadth
A. juncea[c]	not given	0.83	0.74	width at distal margin
A. palmata[a]	~0.80	0.76	0.68	apical breadth
A. septentrionalis[f]	0.60	0.66	0.59	greatest breadth
A. sitchensis[b]	0.80	0.77	0.69	greatest breadth
A. subarctica[a]	not given	not illustrated		labium like *A. juncea*
A. subarctica[c]	not given	0.84	0.76	distal width
A. umbrosa[a]	~0.75	0.66	0.61	apical breadth
A. verticalis[d]	0.75	0.75	0.67	distal width
R. californica[a]	not given	0.91	0.79	apical breadth
R. multicolor[a]	~0.89	0.89	0.79	apical breadth

[a]Walker 1912
[b]Walker 1922
[c]Walker 1934
[d]Walker 1941
[f]Whitehouse 1941

prementum at the base/distal or greatest width (10); the ratio of the width of the prementum at the base/length (2); similarity of the labium or head to other species (5); and a description of the shape of the lateral margins or sides of the folded labium or prementum (14). Walker (1958) referred to distal or greatest width of the labium in a fashion similar to his earlier works, referring to distal width for seven species, greatest width for three species, and for four others he stated that the distal width equaled the greatest width (Table 3). Thus, he appeared to tailor the description of the labium of each species to best meet what he judged to be the most diagnostic aspects for that species.

For the nine species for which Walker (1958) indicated that the greatest or distal width of the labium was divided by the length of the folded labium (see Table 3), his stated ratios were closer in all cases to the calculated ratios that included the postmental hinge that we derived from both his illustrations and the specimens in our collections (Table 4). This result leaves little doubt that when Walker (1958) referred to the folded labium, he meant the prementum plus the ventrally visible portion of the postmental hinge.

Among the five species for which Walker (1958) indicated that the greatest or distal width was divided by the length of the prementum, he stated a

Table 3. Descriptions of the length, width, and shape of the labium of 16 species of *Aeshna* and *Rhionaeschna* excerpted from Walker (1958).

Species	**Labium description**
A. canadensis	… folded labium about five-eighths as broad at base as at distal articulation, the greatest width being equal to about 70 percent of the length; proximal three-fifths with sides slightly divergent distad and slightly convex; distal two-fifths of sides more decidedly convex; …
A. clepsydra	… folded labium widest at distal end, width here 65 percent of the length, width at base of prementum seven-elevenths of its length; distal two-fifths of lateral margins about as convex as in *canadensis***;** …
A. constricta	Folded labium reaching mesocoxae, width at base of prementum slightly more than half the distal width, which is equal to about three-quarters of the length; proximal four-sevenths of prementum widening considerably, the sides straight, distal three-sevenths widening more rapidly, the sides moderately arcuate; …
A. eremita	… distal width of folded labium 70 percent of length; proximal width of prementum 61 percent of distal width; lateral margin of prementum strongly arcuate in the distal 36 percent of its length; …
A. interrupta	**F**olded labium a little narrower than in *eremita***,** the distal width being 65 percent of the length, as compared with 70 in *eremita***;** *width of prementum at base 58 percent of distal width, the convexity of the lateral margin in the distal three-eighths of its length less pronounced than in eremita.*
A. juncea	… folded labium widest a little before the distal articulation, the width here being nearly two-thirds of the length, lateral margins slightly divergent in the proximal three-fifths, strongly convex distally, …
A. palmata	… folded labium reaching a little beyond the middle of the mesocoxae, its greatest width, at the distal end, equal to about two-thirds of the length, its proximal four-sevenths straight-sided, widening slightly distad; the distal three-sevenths with sides strongly arcuate, …
A. septentrionalis	… folded labium reaching a little beyond the mesocoxae, like that of *umbrosa* in form, proximal width of prementum about half the distal width, which is equal to about two-thirds of its length; sides nearly straight and slightly divergent in proximal three-fifths, strongly arcuate in distal two-fifths; …

Table 3. Continued.

Species	Labium description
A. sitchensis	… folded labium reaching middle of mesocoxae, relatively wide in proximal half, with sides nearly straight and slightly divergent, distally strongly convex, the greatest width well before the palpal articulations, about equal to four-fifths of the length of the prementum; proximal width of which is barely less than two-thirds of its distal width; …
A. subarctica	Head and eyes as in *juncea*; labium with prementum somewhat less widened distally, the lateral margins less strongly sinuate and not converging to the bases of the palpi; proximal width a little more than three-fifths of distal width; …
A. tuberculifera	… folded labium attaining the level of the hind coxae, slightly longer than hind femora, its distal width about 55 percent of the length, basal width of prementum slightly less than half the distal width.
A. umbrosa	Folded labium reaching beyond the bases of the mesocoxae, its greatest width, at distal end, three-fifths of its length, the proximal four-sevenths straight-sided, widening but little distad, the sides distally strongly arcuate; …
A. verticalis	… folded labium widest at distal end, the width here being equal to two-thirds of the length; width at base of prementum slightly more than half its length; sides proximally nearly straight and slightly divergent, in distal three-sevenths moderately convex; …
R. californica	Folded labium reaching as far back as middle of mesocoxae, basal width of prementum a little more than half its distal width, which is a little less than the length; sides somewhat divergent throughout its length, slightly convex in the proximal three-sevenths, almost equally convex but more widely divergent in the distal two-fifths, …
R. multicolor	Folded labium attaining a level of middle of mesocoxae, widening distally throughout its length, particularly in the distal three-sevenths, although this part is less dilated than in most species of *Aeshna*, lateral margins slightly sinuate, basal width of prementum about half its distal width, which equals about eight-ninths of the length; …
R. mutata	Very like that of *A. multicolor*, all parts of the head apparently indistinguishable in the two species.

ratio for four of the species (*A. constricta*, *A. septentrionalis*, *A. sitchensis*, and *R. multicolor*). Among these four species, his stated ratios were closer to our ratios from his illustrations excluding the postmental hinge for two species (*A. sitchensis* and *R. multicolor*), closer to the illustration ratio with the hinge included for one species (*A. constricta*), and about equidistant between the two for another (*A. septentrionalis*) (Table 4). Ratios calculated from our specimens followed the same pattern except for *A. septentrionalis*, for which our ratio excluding the hinge was clearly closer to Walker's stated ratio (Table 4). This analysis indicated that when Walker (1958) referred to the prementum, he likely intended to restrict his measurements to that structure. The single exception (*A. constricta*) could be due to intraspecific morphological variation or an unknown source of methodological error.

Ratios of W(max)/L using both the folded labia and prementums of our specimens were consistently similar to Walker's (1958) for nearly all species (Table 4). We postulate that for those species for which a somewhat larger disparity existed between our ratios and his stated ratios (*A. interrupta* and *A. juncea*) that the differences were more likely due to geographic or individual morphological variation within these species than to either determination or measurement error. Two considerations support this conclusion: 1) differences were noticeable for species that are relatively easy to identify (i.e., *A. constricta* and *A. tuberculifera*) reducing the probability of determination errors, and 2) differences were about equally likely to go in either direction (larger or smaller; Table 4) reducing the probability of systematic methodological errors. We also note that measurements and ratios done independently by the two authors of this paper were invariably similar. These similarities serve to affirm the conclusion that although measurements of the prementum and folded labium must be done with care, they are closely repeatable among workers and will consistently lead to correct species determinations in properly designed couplets of dichotomous keys.

Whether or not the visible portion of the postmental hinge should be included when the labia of *Aeshna* and *Rhionaeschna* nymphs are measured depends on the application and the species involved. Because most recent species keys to these genera are based on Walker (1958), the postmental hinge should be included in labium length measurements for those species for which Walker measured the folded labium and stated a ratio (*A. canadensis*, *A. clepsydra*, *A. eremita*, *A. interrupta*, *A. juncea*, *A. palmata*, *A. tuberculifera*, *A. umbrosa*, and *A. verticalis*). For those species for which Walker measured the prementum to calculate labial width/length ratios and stated a ratio (*A. sitchensis* and *R. multicolor*) only the prementum should be measured. Interpretations of the data for the remaining species are ambiguous because Walker did not give a ratio for *A. subarctica*, *R. californica*, or *R. mutata*, the ratios we measured for *A. septentrionalis* were inconclusive when compared with Walker's stated ratio for that species, and Walker's stated ratio for *A. constricta* was closer to our calculated ratios that included the postmental hinge (folded labium) even though he indicated that he measured the prementum of that species.

When using characteristics of the labium in dichotomous keys to determine species of *Aeshna* and *Rhionaeschna*, it is imperative that workers know what measurement is referred to in the particular key being used. An approximate conversion between the two methods of calculating ratios of labial W(max)/L can be made as follows: ratio calculated when the length of the prementum excluding the postmental hinge is used x 0.88 is approximately equal to the ratio when the length of the folded labium including the visible portion of the postmental hinge is used for species of *Aeshna* and *Rhionaeschna* in North America. We further note that the standard errors of measurement of the labia of our specimens (indicators of measurement variability) were smaller when the prementum was measured without the postmental hinge for 8 of the 16 species (Table 5). Standard

Table 4. Labium ratios (greatest or distal W/L) of exuviae or F-0 nymphs of 16 species of *Aeshna* and *Rhionaeschna* as stated by Walker (1958), as we calculated from measurements of his 1958 illustrations (with and without the postmental hinge), and of nymphs and exuviae in our collections (with and without the postmental hinge; maximum width measured). Underlined ratios (where applicable) are the closer of the pair of ratios from Walker's illustrations, and our specimen measurements, to Walker's stated ratio.

Species	Walker's stated ratios (1958)	Ratios calculated from measurements of Walker's illustrations		Ratios calculated from specimens measured by the authors	
		without hinge	with hinge	without hinge	with hinge
A. canadensis	~0.70	0.76	0.70	0.80	0.70
A. clepsydra	0.65	0.74	0.66	0.77	0.68
A. constricta	~0.75	0.83	0.74	0.89	0.77
A. eremita	0.70	0.80	0.73	0.84	0.73
A. interrupta	0.65	0.80	0.71	0.81	0.71
A. juncea	≤0.67	0.85	0.76	0.81	0.71
A. palmata	~0.67	0.75	0.68	0.79	0.70
A. septentrionalis	~0.67	0.69	0.64	0.65	0.57
A. sitchensis	~0.80	0.77	0.68	0.77	0.67
A. subarctica	none given	0.82	0.75	0.80	0.71
A. tuberculifera	~0.55	0.61	0.55	0.66	0.59
A. umbrosa	0.60	0.69	0.64	0.71	0.63
A. verticalis	0.67	0.75	0.68	0.75	0.66
R. californica	none given[a]	0.96	0.86	0.93	0.80
R. multicolor	~0.89	0.89	0.83	0.90	0.80
R. mutata	none given	0.87	0.78	0.91	0.78

[a]the distal width of the prementum was described as being a little less than the length.

errors were equal between the two forms of length measurement for the other 8 species; in no case was the standard error smaller when the postmental hinge was included in the measurement. Because including the postmental hinge in measurements of the labium evidently adds an unnecessary additional source of potential error, we recommend that workers restrict length measurements to the prementum (Fig. 1; measurement "L1") in future studies of this family.

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Table 5. Mean prementum and folded labium width and length measurements (mm) of reared exuviae, unassociated exuviae, and F-0 nymphs of *Aeshna* and *Rhionaeschna* from specimens measured by the authors (n = 10 for all species; SE in parentheses, in bold when the lower of a pair of length measurements).

Species	**Mean prementum maximum width (Wmax)**	**Mean prementum minimum width (Wmin)**	**Mean prementum length (without postmental hinge)**	**Mean folded labium length (including postmental hinge)**
A. canadensis	4.81 (0.05)	2.87 (0.04)	5.98 (0.07)	6.82 (0.07)
A. clepsydra	4.72 (0.05)	2.69 (0.03)	6.12 (**0.06**)	6.97 (0.07)
A. constricta	5.36 (0.06)	2.62 (0.02)	6.06 (0.04)	6.93 (0.04)
A. eremita	5.84 (0.10)	3.42 (0.06)	6.96 (0.17)	8.00 (0.17)
A. interrupta	4.81 (0.04)	2.60 (0.03)	5.93 (**0.08**)	6.73 (0.09)
A. juncea	4.75 (0.05)	2.61 (0.04)	5.89 (**0.07**)	6.71 (0.08)
A. palmata	4.89 (0.04)	2.41 (0.02)	6.22 (**0.05**)	7.00 (0.06)
A. septentrionalis	3.88 (0.04)	1.96 (0.03)	5.97 (0.08)	6.76 (0.08)
A. sitchensis	3.79 (0.03)	2.03 (0.02)	4.93 (0.04)	5.69 (0.04)
A. subarctica	5.13 (0.04)	3.10 (0.03)	6.38 (0.05)	7.23 (0.05)
A. tuberculifera	4.67 (0.07)	2.24 (0.03)	7.08 (**0.12**)	7.90 (0.14)
A. umbrosa	4.66 (0.07)	2.25 (0.04)	6.60 (**0.09**)	7.37 (1.00)
A. verticalis	4.46 (0.05)	2.43 (0.03)	5.94 (0.07)	6.71 (0.07)
R. californica	4.49 (0.05)	2.54 (0.03)	4.81 (**0.05**)	5.59 (0.06)
R. multicolor	5.11 (0.06)	2.60 (0.03)	5.66 (0.05)	6.42 (0.05)
R. mutata	5.15 (0.04)	2.86 (0.02)	5.68 (**0.04**)	6.57 (0.06)

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