Descriptions and Keys for Ammocoetes of Lampreys from British Columbia, Canada

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Characters useful for the identification of ammocoetes of lampreys found in British Columbia were verified by rearing ammocoetes through metamorphosis to specifically identifiable adults. We developed a key that employs new as well as some previously published features. We showed that published descriptions previously thought to be characteristic of species are unreliable for taxonomy. Counts of trunk myomeres and body proportions were not useful for separating species.

Key words: ammocoetes, taxonomy, identification criteria

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En élevant des ammocètes jusqu'au stade adulte identifiable, en passant par la métamorphose, il a été possible de vérifier les caractères taxonomiques des ammocètes de lamproies rencontrées en Colombie-Britannique. Nous avons préparé une clé reposant sur des caractères à la fois nouveaux et déjà publiés. Nous démontrons que des diagnoses jadis considérées comme étant caractéristiques de l'espèce ne sont pas fiables en taxonomie. Les comptages de myomères du tronc et les proportions du corps ne permettent pas de séparer les espèces.

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LAMPREYS are probably present in most coastal rivers and streams in British Columbia, but little is known about the relative abundance of the various species. There are two anadromous species, the Pacific lamprey, *Lampetra tridentata*, and the river lamprey, *Lampetra ayresi*, and one freshwater parasitic species, *Lampreta macrostoma* (Beamish 1982). All are parasitic on commercially important fishes. One nonparasitic lamprey, *Lampetra richardsoni*, is also widely distributed throughout British Columbia. Observations on the relative abundance of adults in saltwater and returning to spawn in freshwater (Beamish 1980) indicate that the Pacific lamprey is the most abundant of these parasitic lampreys and poses the most serious threat to other fishes.

To assess the impact of lamprey attacks on commercial fishes it is necessary to estimate the abundance of the parasitic species. Initially these estimates can be very approximate, but it is important to know the order of magnitude of lamprey abundance in the various watersheds. Juvenile anadromous lamprey can be specifically identified but it is both technically difficult and expensive to enumerate them during this period. During the larval period, when ammocoetes live burrowed in the mud and sand of the stream bed, they are susceptible to electrofishing and large numbers can be collected: it is during this time that abundance data are easiest to obtain. In preliminary studies Richards (1980) concluded that identification of ammocoetes using published criteria is unreliable. Therefore it was necessary to reevaluate taxonomic criteria for the identification of ammocoetes found in coastal streams of British Columbia. The establishment of reliable characters

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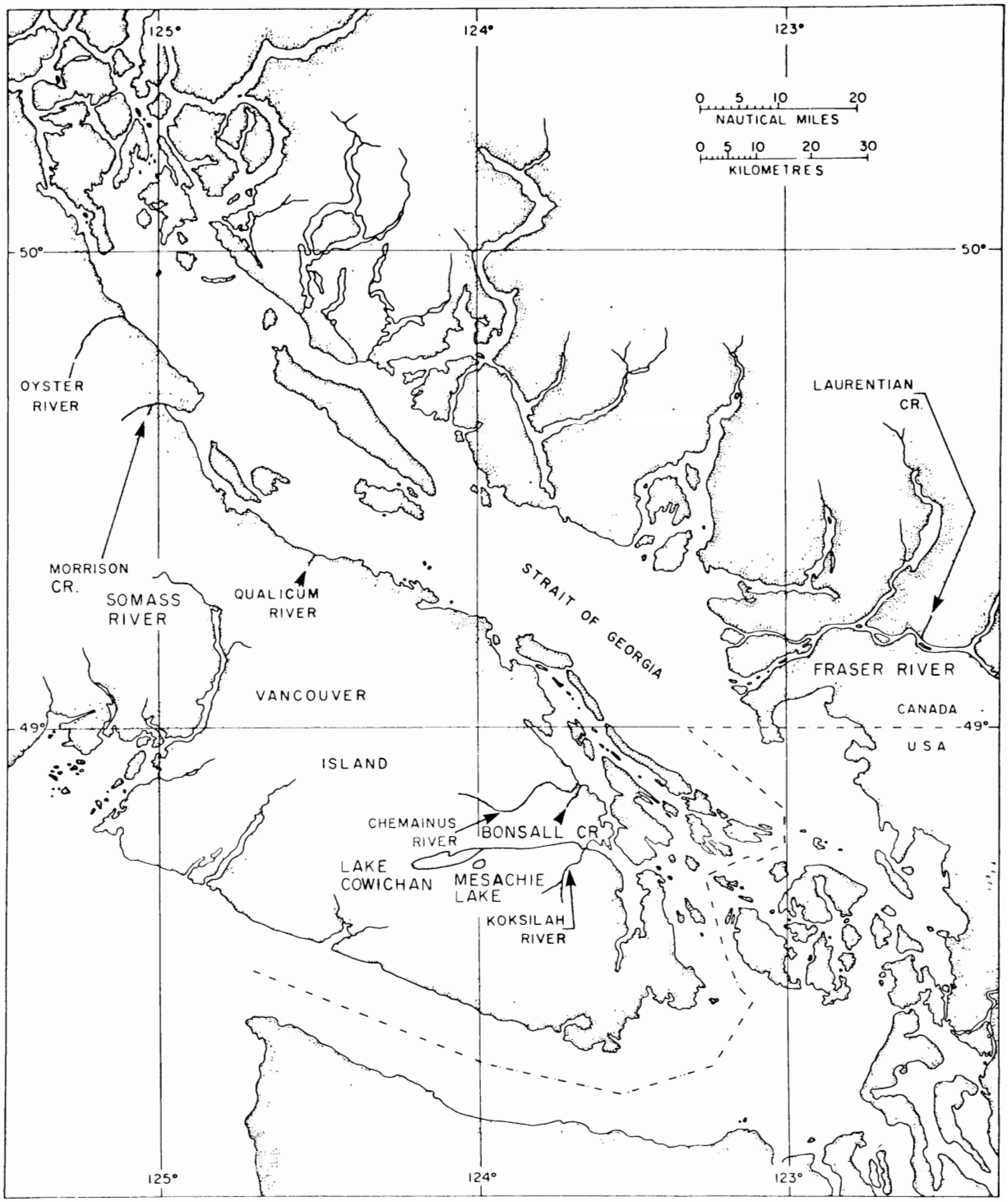

FIG. 1. The lower coast of British Columbia showing the locations of streams where samples of ammocoetes were collected.

required the rearing of ammocoetes to verify the species to which they belonged.

This paper reviews and revises the taxonomy of lamprey ammocoetes in British Columbia. A key is presented that uses characters that are confirmed as being taxonomically significant at the species level.

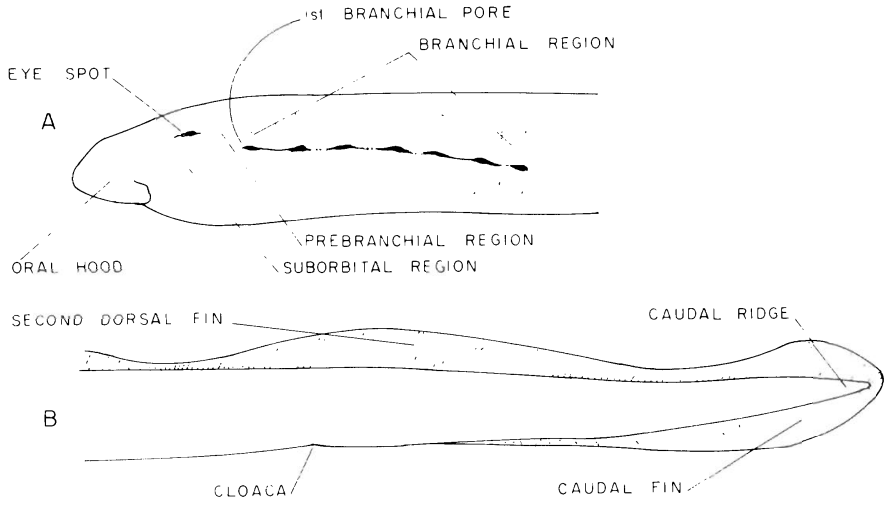

FIG. 2. Drawing of a typical ammocoete showing the external regions used to describe pigmentation patterns (Vladykov 1950). A) Head region, B) Tail region.

Materials and Methods

Most ammocoetes were collected by electrofishing from sites in rivers that were within 5 km of the tidal boundary (Fig. 1). One sample was obtained from Laurentian Creek which enters the Fraser River 30 km from the ocean. Ammocoetes were also collected from a dredging operation in the Fraser River near Mission, British Columbia, 65 km from the mouth of the river. All samples were transported live to the laboratory, anesthetized with tricane methane sulfonate (MS222), measured for total length, and examined for external morphological characteristics. Most were then preserved in 5% formalin and subsequently reexamined. Subsamples of ammocoetes from some collections were held alive in 375-L rearing tanks. The tanks contained a substrate of fine washed sand and were supplied with running dechlorinated fresh water of ambient temperature that fluctuated seasonally from 6 to 20°C. Ammocoetes were fed twice weekly following the procedures of Hanson et al. (1974) until metamorphosis was complete. Metamorphosed lampreys were transferred from freshwater (0‰) to full strength sea water 28–30‰ over a 3-d period to determine if they were *L. ayresi* which can survive in salt water or *L. richardsoni* which cannot.

External pigmentation pattern from various body regions (Fig. 2; Vladykov 1950) was described for both fresh and preserved material.

Pigmentation of the tongue precursor was examined and described following the methodology of Vladykov (1950). The number of trunk muscle myomeres was determined by removing a strip of skin from the left side of the ammocoete and counting the myomeres between the posterior branchial pore and the cloaca (Hubbs and Trautman 1937). The first myomere counted was the one that contained no portion of the last branchial pore and the last myomere was the one whose lower posterior angle lies in part or wholly above the cloacal slit. In some cases the muscles were stained with eosin (Pletcher 1963) to enhance differentiation of the myomeres and myoseptae. Samples of 203 *L. tridentata*, 254 *L. richardsoni* and 50 *L. ayresi* were examined for tongue precursor pigmentation patterns and the number of trunk myomeres.

Body proportions were measured to the nearest 0.1 mm from the left side of the ammocoete using the following definitions from Hubbs and Trautman (1937) and Vladykov (1950): Prebranchial length, tip of snout to the anterior edge of the first branchial pore; branchial length, the anterior edge of the first branchial pore to the posterior edge of the last branchial pore; trunk length, the posterior edge of the last branchial pore to the anterior edge of the cloaca; tail length, the anterior edge of the cloaca to the posterior edge of the caudal fin; total length, the tip of the snout to the posterior edge of the caudal fin. The dentition of postlarval lampreys was examined using a dissecting microscope, and described according to the terminology and definitions which follow Vladykov and Follett (1967).

To establish the size at which pigmentation differences could first be distinguished, we reared *L. ayresi* and *L. richardsoni* ammocoetes from eggs that were fertilized in the laboratory. Eggs were held in trays and floated in tanks containing running dechlorinated water of ambient temperature. Prolarvae were transferred to tanks containing sand substrate and reared on a diet of algae and yeast. During the rearing period, samples of these ammocoetes were collected from the tanks after 3, 12, and 24 mo, then anesthetized and examined for pigmentation pattern. Reared *L. ayresi* ammocoetes were maintained for 2 yr and *L. richardsoni* ammocoetes for 1 yr.

Results

LAMPETRA TRIDENTATA

A sample of 41 ammocoetes (length range 96–144 mm) from the Qualicum River (Fig. 1) collected in July 1977 was identified as *L. richardsoni* on the basis of the pigmentation pattern of the anterior region as described for preserved speci-

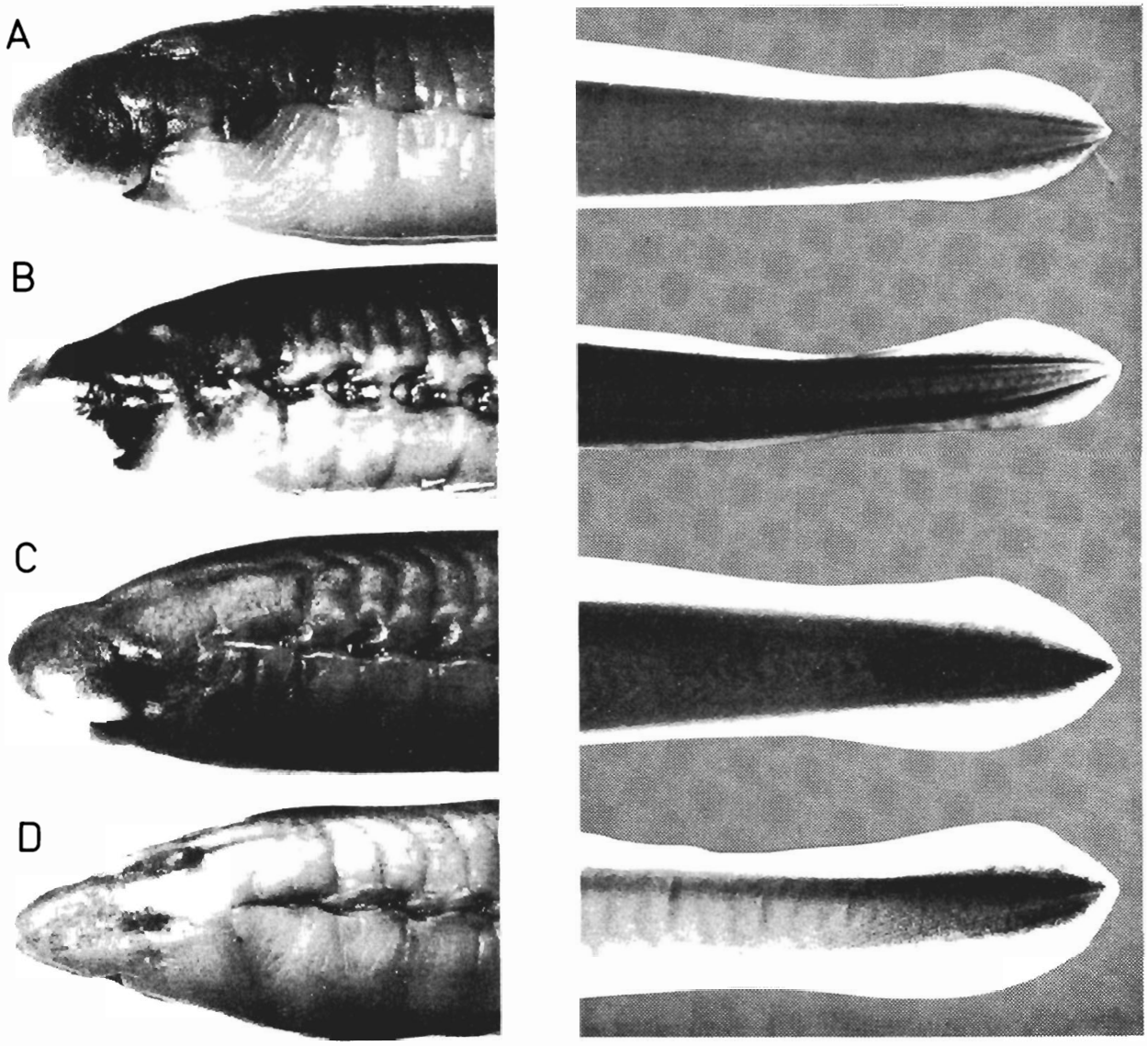

FIG. 3. Head and tail pigmentation of (A) *L. tridentata*, (B) *L. macrostoma*, (C) *L. richardsoni* and (D) *L. ayresi*. Note the light caudal ridge of the *L. tridentata* and *L. macrostoma* ammocoetes, dark tail of *L. richardsoni* and the intermediate condition of *L. ayresi*. The head of *L. ayresi* is more lightly pigmented than the other species. The pattern of pigmentation in the head region of *L. tridentata*, *L. macrostoma* and *L. richardsoni* represents the average condition observed in this study.

mens by Vladykov and Follett (1965) and Pletcher (1963). The ammocoetes were kept alive and in February 1978, six had metamorphosed. The dentition of these postlarval individuals clearly indicated they were *L. tridentata* and not *L. richardsoni*. These observations and the discrepancies between the descriptions of Vladykov and Kott (1976a) and Pletcher (1963) of the head pigment patterns of *L. tridentata* ammocoetes indicated that head pigmentation as previously described may not be suitable for separating *L. tridentata* ammocoetes from other species.

Reexamination of the external pigmentation of live as well as preserved specimens collected from various streams revealed two distinctly different tail patterns associated with the posterior termination of the notochord in the caudal fin. The termination of the notochord and overlying tissues form a lateral thickening in the tail region and will be referred to as the caudal ridge (Fig. 2).

The specimens in the Qualicum River sample (now shown to contain at least some *L. tridentata* ammocoetes) were reexamined and all were observed to possess a common pigmentation pattern in the tail region. The caudal ridge was lightly pigmented, surrounded by a border of much darker pigmentation which uniformly faded to a light grey towards the peripheral margins of the caudal fin (Fig. 3A). An

TABLE 1. Body proportions of *L. tridentata* ammocoetes from various streams in British Columbia. Values expressed in percent total length ±1 SD.

	Total length (mm)												
	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149
Number	3	3	16	15	16	5	18	21	47	41	29	23	5
Prebranchial													
Qualicum	—	—	—	—	—	—	9.6±1.4	8.5±0.4	8.3±0.4	8.3±0.4	7.6±0.5	7.5±0.4	6.8±0.2
Oyster	13.0±0.5	12.1	11.2±0.8	10.3±0.5	9.7±0.2	—	—	8.5±0.3	8.0±0.4	7.8±0.4	7.6±0.2	7.3±0.3	6.9
Koksilah	—	—	—	—	—	—	—	8.6	8.7±0.2	8.1±0.1	8.1±0.4	7.8	—
Chemainus	—	11.6±0.5	10.8±0.3	10.2±0.2	9.7±0.3	9.5±0.3	8.7±0.4	8.5±0.4	8.3±0.4	8.0±0.1	7.6	—	—
mean	13.0	11.8	11.0	10.2	9.7	9.5	9.1	8.5	8.3	8.0	7.7	7.5	6.8
Branchial													
Qualicum	—	—	—	—	—	—	12.6±0.2	12.4±0.6	12.8±0.5	12.1±0.6	11.7±0.5	11.9±0.3	10.6±0.2
Oyster	15.8±0.6	15.0	14.3±0.1	13.8±0.4	13.2±0.1	—	—	13.1±0.5	12.7±0.6	12.4±0.6	12.0±0.3	12.1±0.6	11.4
Koksilah	—	—	—	—	—	—	—	12.7	12.9±0.4	12.5±0.4	12.2±0.4	11.7	—
Chemainus	—	14.4±0.7	14.2±0.6	12.8±0.7	13.6±0.8	13.2±0.3	13.3±0.5	12.7±0.6	12.7±0.6	12.3±0.6	11.4	—	—
mean	15.8	14.7	14.2	13.8	13.4	13.2	12.9	12.7	12.8	12.3	11.8	11.9	11.0
Trunk													
Qualicum	—	—	—	—	—	—	49.8±0.2	49.6±0.8	49.9±0.2	50.0±0.8	50.9±0.9	50.2±0.8	51.2±1.1
Oyster	55.3±1.5	53.5	50.7±0.5	50.1±1.8	49.5±1.2	—	—	50.2±0.8	51.0±1.1	50.2±1.2	50.5±1.1	50.6±1.2	52.1
Koksilah	—	—	—	—	—	—	—	48.5	49.0±0.6	49.4±0.9	48.8±0.7	49.2	—
Chemainus	—	49.5±0.3	50.5±1.8	49.4±0.9	49.4±1.0	49.7±0.4	50.0±0.8	49.6±1.3	49.6±0.9	49.1±0.8	50.1	—	—
mean	55.3	51.5	50.6	49.7	49.4	49.7	49.9	49.5	49.9	49.7	50.1	50.0	51.6
Tail													
Qualicum	—	—	—	—	—	—	28.2±0.7	29.3±0.9	29.1±1.3	29.9±1.3	29.7±1.3	30.1±0.6	30.7±0.9
Oyster	18.4±0.8	22.9	24.6±0.3	26.0±1.1	26.7±0.2	—	—	28.6±0.2	29.0±0.8	30.1±1.2	30.0±0.6	30.2±0.7	29.4
Koksilah	—	—	—	—	—	—	—	29.6	29.8±0.3	29.8±0.9	30.8±0.5	31.3	—
Chemainus	—	23.0±1.3	24.8±1.5	25.9±1.1	27.2±0.8	27.9±0.3	28.5±0.9	29.8±1.1	30.9±0.8	30.3±1.0	30.5	—	—
mean	18.4	22.9	24.7	25.9	26.9	27.9	28.3	29.3	29.5	30.0	30.2	30.5	30.3

TABLE 2. Muscle myomere counts for ammocoetes of *L. richardsoni*, *L. tridentata*, and *L. ayresi* from several streams in British Columbia (± 1 SD).

Species	Location	Sample size	Number of myomeres												Mean ± SD
			58	59	60	61	62	63	64	65	66	67	68	69	
L. richardsoni	Oyster R.	108	2	2	11	23	33	27	7	2	1	—	—	—	61.9±1.4
	Morrison Cr.	78	—	—	—	10	13	31	17	4	2	1	—	—	63.0±1.2
	Bonsall Cr.	25	—	—	—	—	—	5	6	5	7	2	—	—	64.8±1.3
	Koksilah R.	26	—	—	—	1	4	9	10	1	1	—	—	—	63.4±1.1
	Laurentian Cr.	40	—	—	—	—	7	17	8	4	2	2	—	—	63.6±1.3
Total		277	2	2	11	34	57	89	48	16	13	5	—	—	62.9
L. tridentata	Oyster R.	42	—	—	—	—	—	1	5	12	13	10	1	—	65.6±1.2
	Qualicum R.	63	—	—	—	—	—	—	1	9	24	19	9	1	66.5±1.0
	Koksilah R.	61	—	—	—	—	—	1	3	16	21	16	4	—	65.9±1.0
	Chemainus R.	37	—	—	—	—	—	—	—	12	13	11	1	—	66.0±0.9
Total		203	—	—	—	—	—	2	9	49	71	56	15	1	66.1
L. ayresi	Fraser R.	50	—	—	—	—	—	3	10	19	13	5	—	—	65.1

additional sample of 50 ammocoetes (length range 116–142 mm) collected from the Qualicum River July 1978 also exhibited a lightly pigmented caudal ridge. A sample of 25 was preserved for subsequent examination while the remainder were held alive. In October 1978, 48% were nearing the completion of metamorphosis and, based on the dentition pattern, these individuals were positively identified as *L. tridentata*. The remaining ammocoetes metamorphosed the following year and were also *L. tridentata*.

The head pigmentation patterns of *L. tridentata* were variable and not suitable for separating *L. tridentata* and *L. richardsoni*, contrary to views previously reported by Pletcher (1963) and Vladykov and Kott (1976a). In *L. tridentata* the prebranchial blotch was not always present, nor was there always an unpigmented zone above the branchial pores (Fig. 3A). The upper lip and suborbital areas are moderately pigmented and appear grey when preserved (Fig. 3A) or grey-brown in live samples. The degree of pigmentation in the branchial area was difficult to differentiate in live material.

The body proportions of *L. tridentata* ammocoetes expressed as a percent of total length were found to vary according to the total length (Table 1). The size of the prebranchial region relative to total length is larger in smaller individuals, ranging from 13.0 to 6.8% as total length increased from 24 to 145 mm. The proportion of the branchial region to total length is also inversely related to length. The mean proportion of branchial length to total length for ammocoetes in the 20–29 mm length interval was 15.8% compared to 11.0% for ammocoetes in the 140–149 mm range. Decreases in the relative size of the prebranchial and branchial areas were accompanied by increasing trunk and tail proportions. After an initial decrease in the very small length intervals the relative trunk length increased from 49.4 to 51.6% of the total length over a length interval of 65–145 mm. The most noticeable example of allometric growth occurred in the tail region which increased from 18.4 to 30.3% of the total length over the 25–145 mm length intervals. This change occurred mostly among the smaller size classes.

The differences among the number of myomeres (65.6, 65.9, 66.0, 66.5) found in *L. tridentata* ammocoetes (Table 2) from four streams were not significant (*t*-test, $P \geq 0.05$).

The area immediately surrounding the tongue precursor bulb and the associated ridge extension were pigmented (Fig. 4A); the bulb structure was not pigmented.

LAMPETRA RICHARDSONI

Ammocoetes that were not *L. tridentata* had a different tail pigmentation pattern. The taxonomic significance of this second tail pigmentation pattern was studied from a sample of ammocoetes and metamorphosed ammocoetes that were collected from Laurentian Creek (Fig. 1) in November 1977. The tail pattern consisted of intense pigmentation in the area of the caudal ridge, appearing almost black in many cases (Fig. 3C). The extent of pigmentation radiating out to the caudal fin was variable, often giving the caudal fin a mottled appearance in the peripheral region. This pattern was clearly different from that possessed by *L. tridentata* ammocoetes from Qualicum River. The dentition pattern of the metamorphosed ammocoetes in the sample also supported the conclusion that these individuals were not *L. tridentata*. These ammocoetes were tentatively identified as *L. richardsoni*, however, the possibility that this sample might also be a mixture of *L. richardsoni* and *L. ayresi* was not discounted because we had yet to develop criteria for identifying *L. ayresi*. A subsample of 37 ammocoetes (length range 135–213 mm) was held alive until postlarval examination could confirm our identification. By 1980 all ammocoetes in this sample metamorphosed, spawned in the rearing tank, and died. This behavior in addition to the inability of juvenile forms to osmoregulate in salt water confirmed that this second tail pattern was characteristic of *L. richardsoni*.

The head pigmentation of *L. richardsoni* ammocoetes was generally darker than *L. tridentata* when comparing preserved material, however, reliable identification could not be based on head pigmentation. The suborbital and branchial areas are moderately pigmented giving way to light pigment in the ventral region (Fig. 3C). The prebranchial area was moderately to strongly pigmented while the upper lip was

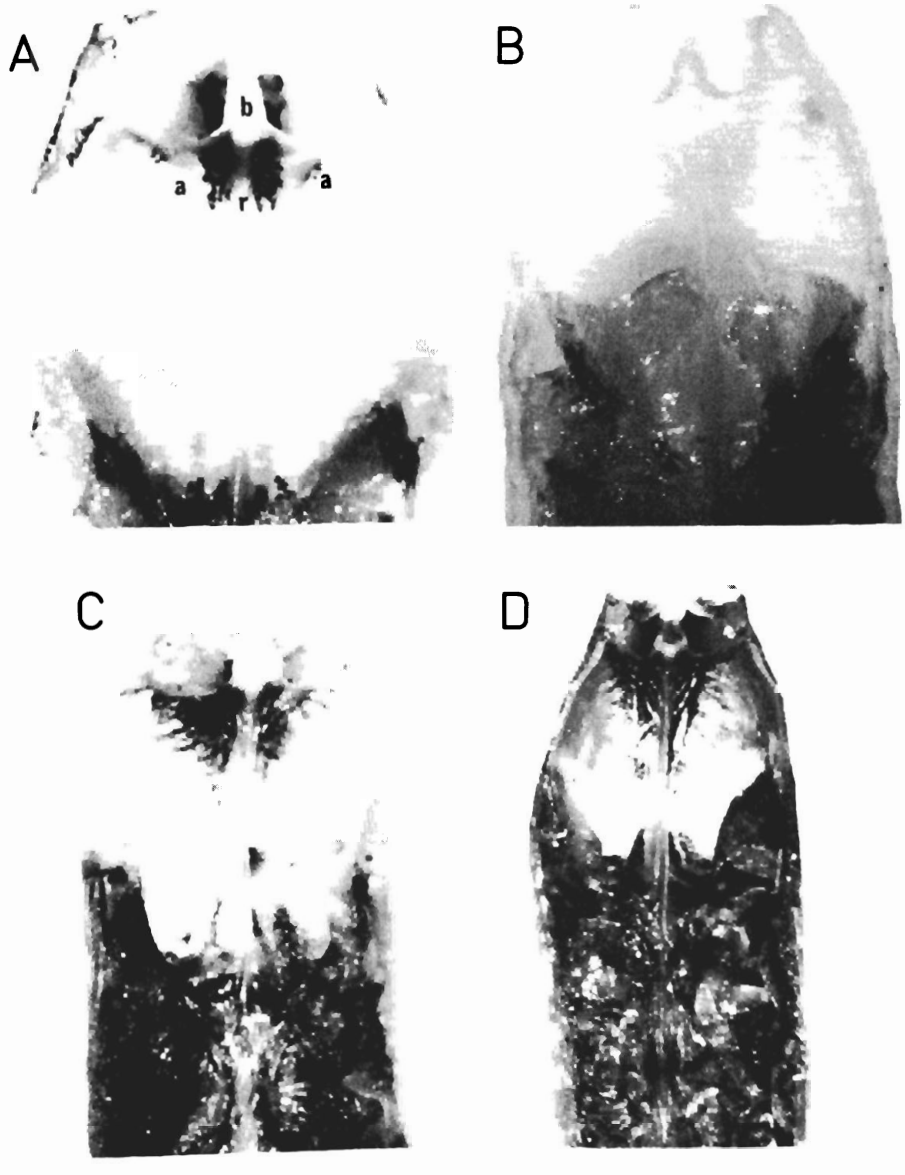

FIG. 4. The pigmentation of the tongue precursor and surrounding area for (A) *L. tridentata*, (B) *L. ayresi*, (C,D) *L. richardsoni*. Figures C, D illustrate the degree of variability which was observed. a, surrounding area; b, tongue precursor bulb; r, tongue precursor ridge.

moderately pigmented.

The changing relative size of body proportions noted among *L. tridentata* ammocoetes was also apparent among *L. richardsoni*. The relative proportion of the prebranchial region expressed in terms of total length decreased from 8.7 to 7.1% as the total length increased from 85 to 185 mm (Table 3). Similarly, the relative size of the branchial region also decreased. Ammocoetes in the 80 to 89 mm interval had a branchial length of 13.8% compared to 11.5% total length for those in the 180–189 mm interval. The relative proportion of the trunk and tail regions increased with increasing total length. Mean trunk lengths for 10 mm intervals ranging from 85 to 185 mm increased from 50.4 to 52.8% while the size of the tail region increased from 27.4 to 28.7% of the total length.

The mean number of myomeres of *L. richardsoni* ammocoetes (Table 2) from five streams (61.9, 63.0, 63.4, 63.6, 64.8) was less than *L. tridentata* but individual counts were variable ranging from 58 to 67. Because of this variation, myomere counts were of little use for identifying ammocoetes.

Pigmentation of the tongue precursor structure and surrounding area in *L. richardsoni* ammocoetes was variable but generally more extensive in the area surrounding the tongue

TABLE 3. Body proportions of *L. richardsoni* ammocoetes from various streams in British Columbia. Values expressed in percent total length ±1 SD.

	Total length (mm)										
	80–89	90–99	100–109	110–119	120–129	130–139	140–149	150–159	160–169	170–179	180–189
Number	3	19	44	59	45	27	22	20	12	2	2
Prebranchial											
Bonsall	—	7.5±0.6	8.3±0.5	7.7±0.7	7.4±0.2	7.5±0 3	7.3±0.2	7.4±0.2	7.1±0.1	—	—
Laurentian	—	—	—	—	8.1	7.5	7.7±0.3	7.2±0.3	7.0±0.4	6.8±0.2	7.1±0 3
Koksilah	—	—	—	—	8.2±0.1	7.7±0.6	7 9±0 5	7.8±0.7	7.1±0.4	—	—
Oyster	8.7±0.2	8.5±0.5	8.4±0.3	8.1±0.6	7.9±0.4	7.7±0.3	7.7	7.6±0.1	—	—	—
Morrison	—	9 3±0.4	8.9±0.3	8.6±0.3	8.4±0.2	8.2±0.3	7.9	—	—	—	—
mean	8.7	8 4	8 5	8.1	7.9	7.7	7.7	7 5	7.1	6.8	7.1
Branchial											
Bonsall	—	13.4±0.2	13.4±0.5	13.3±0.2	12.2±0.4	13.0±0.2	12 3±0 4	12.5±0.4	11.7±0.1	—	—
Laurentian	—	—	—	—	12.3	12.6	11.5±0 5	11.7±1.0	11.5±0.4	11.3±0.1	11.5±0.7
Koksilah	—	—	—	—	12.6±0.3	11.9±0.2	12.1±0.4	12 3±0.8	11.0±0.5	—	—
Oyster	13.8±0.6	13 1±0 5	13 1±0.6	13.1±0.7	12.7±0.6	12.7±0.6	13.4	12.7±0 3	—	—	—
Morrison	—	13.0±0.7	13 2±0 4	12.8±0.5	12.5±0.6	12.6±0.6	11.7	—	—	—	—
mean	13.8	13.2	13.2	13 1	12.5	12.6	12.2	12.3	11.4	11.3	11.5
Trunk											
Bonsall	—	53.4±0.9	51.4±0.8	52.2±0.4	52.2±0.4	52.3±0.8	52.8±0.7	53 0±1.0	53.3±0.1	—	—
Laurentian	—	—	—	—	52.4	51.5	53.4±0.1	54.2±0.8	54.1±1.3	52.6±1.1	52.8±1.3
Koksilah	—	—	—	—	51.2±0.3	51.5±1.3	51.1±1.2	51.9±0.6	53 4±0.6	—	—
Oyster	50.4±1.7	49.6±1.0	50.3±1 9	49 7±1.7	50.4±1.5	51.2±0.8	51.9	50.5±1.1	—	—	—
Morrison	—	49.1±0.7	50.2±1.1	50 6±1 3	51.0±1.3	51.3±1.5	51.4	—	—	—	—
mean	50.4	50.7	50.7	50.8	51 4	51.6	52.1	52.4	53.6	52 6	52.8
Tail											
Bonsall	—	26 4±0 3	26.7±1.7	27.0±1.2	28.1±0.3	27.5±0.5	27.3±0.6	27.3±1.0	27 5±0.5	—	—
Laurentian	—	—	—	—	27.0	28.8	27.2±1.8	27.7±0.6	27 9±1 2	28.9±0.4	28.7±1.4
Koksilah	—	—	—	—	28.5±0.5	28.2±1.5	29.6±1.4	28.5±1.0	29.2±0.7	—	—
Oyster	27.4±0.6	28.3±0.8	28.4±1.3	28 8±1 1	29.1±1.3	28.7±1.2	29.2	28.9±0.9	—	—	—
Morrison	—	28.0±0.6	27.9±1.0	28.1±1.1	28 2±0 6	28.2±0.7	29.1	—	—	—	—
mean	27.4	27.6	27.7	28.0	28 2	28 3	28.5	28.1	28.2	28.9	28 7

TABLE 4. Body proportions of *L. ayresi* ammocoetes from the Fraser River, in British Columbia. Values expressed as percent total length ±1 SD.

	Total length (mm)				
	70–79	80–89	90–99	100–109	110–119
Number	9	18	30	31	11
Prebranchial	7.7±0.3	8.3±0.4	7.5±0.4	7.3±0.3	7.3±0.5
Branchial	13.8±0.6	13.7±0.4	13.2±0.5	13.1±0.4	12.5±0.4
Trunk	52.7±1.1	52.3±0.9	52.1±1.0	52.7±0.8	52.1±1.3
Tail	26.5±1.0	26.8±0.8	27.1±0.7	26.8±0.9	27.6±1.0

precursor in *L. richardsoni* than *L. tridentata* (Fig. 4A, C–D). While in some cases the degree of pigmentation of tongue precursor structures could be used to separate these two species, we recommended it only be used as a secondary characteristic to tail pigment patterns.

Collections of live ammocoetes from the Oyster and Somass rivers (Fig. 1) were identified as either *L. tridentata* or *L. richardsoni* using tail pigmentation patterns. Species from each river were reared separately and in all cases the ammocoetes metamorphosed into the expected species.

LAMPETRA AYRESI[2]

In May 1980, samples of ammocoetes and juvenile lampreys were collected from the Fraser River. The juveniles were identified as *L. ayresi* on the basis of sharp cornified teeth, silver lateral body pigmentation, and the immature condition of the gonads. These characters were not found in samples of juvenile *L. richardsoni* at this time of year.

The tail pigmentation of ammocoetes in the Fraser River sample had less pigmentation than *L. richardsoni* and while many had a caudal ridge that was uniformly darkly pigmented, some had a light caudal ridge similar to *L. tridentata* (Fig. 3D). We consider that the tail pigmentation pattern should be accepted as variable but in general to be intermediate between *L. richardsoni* and *L. tridentata*. The pigmentation in the head region was reduced and very different from the other species, giving these ammocoetes a lighter appearance than either *L. richardsoni* or *L. tridentata* (Fig. 3D). The suborbital, prebranchial and branchial areas were unpigmented while the area anterior to the eye spot contained the most pigment. The most startling feature of the head pigmentation was the thin dark streak immediately anterior to the eye spot and the dark line that extends posteriorly from the eye spot to a position above the first branchial pore. The other species have this dark line posterior to the eye spot but its prominence is greatly accentuated in *L. ayresi* because of the absence of surrounding pigmentation. This pattern of pigmentation was consistent with a previously published description of *L. ayresi* ammocoetes (Vladykov and Follett 1958), therefore these ammocoetes were tentatively identified as *L. ayresi*. A subsample of 180 ammocoetes (length range 37–122 mm) was held alive and fed as previously described. In January 1981, five postlarval individuals were examined and identified as *L. ayresi*. Unlike juvenile and adult *L. richardsoni* these lampreys had strong sharp dentition.Three of the five juveniles were able to osmoregulate in salt water. The two that died during the transfer into salt water were extremely small and appeared emaciated. The dentition of these lampreys and their ability to survive in salt water confirmed that they were *L. ayresi*.

Changes in the relative proportions of the various body regions with respect to total length were also evident among *L. ayresi*. The relative sizes of the prebranchial and branchial regions were inversely related to total length. Mean length of the prebranchial region for 10 mm length intervals from 75 to 115 mm decreased from 7.7 to 7.3% (Table 4). Similarly, the proportion of relative branchial length to total length decreased from 13.8 to 12.5%. Little change occurred in the size of the trunk region which varied from 52.1 to 52.7% of the total length. The proportion of tail length to total length increased from 26.5% in the 70–79 mm length interval to 27.7% in the 110–119 mm length interval. Myomeres from 50 *L. ayresi* ammocoetes ranged from 63 to 67 with a mean value of 65.1 (Table 2).

As noted by Vladykov and Follett (1958), the tongue precursor in *L. ayresi* ammocoetes had a bulb, ridge, and surrounding area that were completely devoid of pigment (Fig. 4B). This unpigmented condition clearly separates *L. ayresi* from the other two species examined in this study.

Unfortunately it was not possible to maintain the reared *L. ayresi* and *L. richardsoni* beyond 2 yr. The intention was to compare pigmentation patterns annually to determine if pigmentation pattern could be used to separate these species during early development. It was possible to show that the head pigmentation pattern of *L. ayresi* and *L. richardsoni* ammocoetes was established during the first year. The pigmentation in the tail region that was characteristic of larger ammocoetes was not prominent in the first year for either species or in the second year for *L. ayresi*.

Discussion

Some of the published taxonomic criteria for the three species of lamprey ammocoetes examined during this study were found to be inadequate for species identification, particularly when samples were alive. The head pigmentation pattern we observed for *L. tridentata* differed from that described by Vladykov and Kott (1976a). They described an unpigmented band above the branchial pores as being a characteristic which distinguished *L. tridentata* from other closely related species. The *L. tridentata* ammocoetes we examined

[2]The 4-cm juvenile river lamprey recorded in Beamish (1980, p. 1908, Table 1) is unavailable for confirmation and is probably an error; however, we do have a specimen measuring 69 mm.

TABLE 5. A key to ammocoetes in coastal streams in British Columbia. Arrows indicate key features.

1. Tail lightly pigmented in the caudal ridge area; body and head extensively pigmented 3

2. Tail darkly pigmented in the caudal ridge area; or tail lightly pigmented and body and head with reduced pigmentation 4

3. Reduced pigmentation around tongue precursor structure; pigmentation in the suborbital area reduced; may have unpigmented spot above first branchial pore ..... *Lampetra tridentata*[a]

Lampetra macrostoma

4. Area surrounding the tongue precursor structure heavily pigmented; extensive pigmentation in the branchial, prebranchial, and suborbital area..... *Lampetra richardsoni*

5. Reduced pigmentation in the branchial, prebranchial, and suborbital area; prominent line behind eye; area surrounding tongue precursor structure unpigmented ..... *Lampetra ayresi*

[a]*Lampetra* (*Entosphenus*) *tridentata* is the common representative, however, the ammocoetes from Mesachie Lake and Lake Cowichan (Fig. 1) could be *Lampetra macrostoma* or *Lampetra tridentata*. Studies to date indicate that ammocoetes found in these two lakes have been *Lampetra macrostoma*.

clearly showed that in many cases pigment in the branchial region extended down to the branchial pores. Pletcher (1963) described a broad unpigmented blotch anterior and dorsal to the first branchial pore as a characteristic distinguishing *L. tridentata* from other species. Our study showed that this character was variable and should therefore not be used as a primary identifying character.

The heavy pigmentation we found in the suborbital and prebranchial region of *L. richardsoni* ammocoetes is in agreement with the findings of Pletcher (1963) and Vladykov and Follett (1965). However, identification of this species on the basis of this pigmentation was shown not to be possible because there was no consistent difference between *L. tridentata* and *L. richardsoni*.

The pigmentation pattern in the tail region is the only acceptable external character distinguishing *L. tridentata* from *L. richardsoni* ammocoetes and is useful whether the material is alive or preserved. There is no difficulty in interpreting the distinctive light caudal ridge, characteristic of *L. tridentata* ammocoetes. The pigmentation of the tails of *L. ayresi* and *L. richardsoni* can be similar and other characters are required for separating these species.

The results of this study validated the earlier description by Vladykov and Follett (1958) that stated reduced head pigmentation was an identifying criterion for *L. ayresi* ammocoetes. The reduced pigmentation in all areas of the head, except the dorsal surface and around the eye spot, was easily distinguishable from the predominantly heavy pigmentation on *L. richardsoni* ammocoetes.

Vladykov and Follett (1958) described the tail pigmentation patterns for *L. ayresi* and *L. fluviatilis* and claimed that the reduced pigmentation in the tail of *L. fluviatilis* was a

suitable character for separating these two species. The separation of these two species was not reexamined in this study, however, the illustration of the tail pigmentation pattern provided by Vladykov and Follett (1958) for *L. ayresi* is an extreme condition, identical to *L. tridentata*, and not the common pattern in our samples.

If preserved material is being examined it is possible to look at additional taxonomic characters that are useful for identification. The pigmentation of the tongue precursor was useful for separating *L. ayresi* from *L. richardsoni* and *L. tridentata*; *L. ayresi* ammocoetes are distinguishable by the absence of pigmentation in this region. The reduced pigmentation around the tongue precursor structure in *L. tridentata* ammocoetes compared to *L. richardsoni* ammocoetes was consistent and useful for separating these species if there is doubt about tail pigmentation.

The number of myomeres and body proportions of ammocoetes were not useful characters for separating species because of the variation in counts and measurements. For example, the mean myomere values of *L. richardsoni* ranged from 61.9 for Oyster River ammocoetes to 64.8 for Bonsall Creek ammocoetes (Table 2). This is also inconsistent with the work of Vladykov and Follett (1965). They examined 121 ammocoetes from British Columbia and Washington and determined a mean of 60.7 myomeres, much lower than in any of the stream populations we examined. Our values were in closer agreement to the mean of 62.3 myomeres determined by Pletcher (1963) for ammocoetes collected in British Columbia.

Variation in the relative body proportions of ammocoetes of *L. richardsoni* occurred among samples from various rivers. This, in addition to the problem of allometric growth among lampreys, limits the usefulness of body proportions as identifying criteria. Meaningful comparisons of body proportions can only be made between similar sized intervals, and it is unknown at this time if age as well as size is important. Even when similar sized individuals are compared the measurements overlap significantly for the different species.

Interestingly intraspecific variation in the number of myomeres and body proportions was not as apparent among *L. tridentata* ammocoetes as they were for *L. richardsoni*. The difference between mean myomere counts of *L. tridentata* ammocoetes from the four rivers examined was not significantly different (t-test, $P \geq 0.05$). The pooled overall mean of 66.1 was in agreement with the findings of Pletcher (1963) yet lower than 67.6 and 68.7 reported by Vladykov and Kott (1976a) and Vladykov and Kott (1976b), respectively. It is possible that regional differences exist in *L. richardsoni* populations as a result of the isolated distribution of these nonparasitic freshwater species. This is in contrast to *L. tridentata* which may interbreed as a consequence of an absence or a breakdown in homing during its spawning migration from the marine environment. Meristic variation among *L. ayresi* ammocoetes could not be examined because only one source of ammocoetes was available.

In another study, *L. macrostoma* ammocoetes could not be distinguished from *L. tridentata* ammocoetes (Beamish 1982). Ammocoetes were reared through metamorphosis and confirmed to be *L. macrostoma*. The pigmentation was much darker and the ammocoetes grew to larger sizes, however, the pigmentation patterns of these ammocoetes were not sufficiently different to distinguish them from *L. tridentata* (Fig. 3B). Because the distribution of *L. macrostoma* appears restricted to a few freshwater lakes we suggest that until suitable characters can be found, ammocoetes from these watersheds should be considered to be either *L. macrostoma* or *L. tridentata*.

Vladykov and Kott (1976a) also found that the head pigmentation pattern was similar among ammocoetes of species that were considered to be derivatives of *L. tridentata*. In their report they describe a broad unpigmented band above the branchial pores in *L. tridentata* as a suitable character for separating *L. tridentata* from three related species but were unable to separate the three related species. Our rearing studies showed that this character is variable and therefore should not be used to separate *L. tridentata* ammocoetes or its derivatives.

A summary of the criteria for the identification of live and preserved ammocoetes from coastal streams of British Columbia is presented in a key in Table 5.

The ability to identify lamprey ammocoetes is a key step in attempting assessments of the relative biomass of the various species. Knowledge of the relative biomass of the major parasitic species is necessary before the impact of lampreys on commercial fisheries can be estimated.

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