

The Leech *Haemopsis lateromaculata* (Hirudinea: Haemopidae): Its North America Distribution and Additional Notes on Species Description

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The geographic range of *Haemopsis lateromaculata* Mathers 1963 (Hirudinea: Haemopidae) is extended across North America. Its distribution in the coastal region of Alaska and British Columbia suggests a coastal Pleistocene refugia separate from the populations in the lower United States and suggests that *H. lateromaculata* and the Eurasian *H. sanguisuga* Linnaeus 1758 are sister taxa. Support of the identification and geography is based on the anatomical positions of the reproductive organs in *H. lateromaculata* and *H. marmorata* Say 1824. The variations within these species are described, noting that no specific variation was confined to a geographical region.

Key Words: leech, *Haemopsis lateromaculata*, description, taxonomy, distribution, North America.

In an effort to understand the limits of leech (Hirudinea) fauna distribution in western North America, a geographical study defined by hydrological basins was undertaken and is still in progress. The report herein describes a taxonomic problem with *Haemopsis marmorata* (Say 1824) in western North America, a species known to be difficult to distinguish by external characteristics from *H. grandis* (Verrill 1874) (Sawyer 1972) and *H. lateromaculata*. Four populations of *Haemopsis* were found without teeth and these populations were initially identified as *H. grandis* (Hovingh 1993). Examination by dissection revealed that the penis sheaths of these populations were *H. marmorata* and that these specimens had jaws. As a result of this identification problem, the penis sheaths of all mature *Haemopsis* were examined.

In examining the reproductive organs of *Haemopsis*, it became apparent that *H. lateromaculata* specimens in museum collections had often been misidentified as *H. marmorata*. A study of Utah (Beck 1954) and Alaskan (Moore and Meyer 1951) *Haemopsis* vouchers deposited in the United States National Museum (USNM) contained several lots identified as *H. lateromaculata*. Three lots of specimens that were collected from British Columbia and Newfoundland, two of which were identified by J. Madill as *H. lateromaculata* plus one unidentified due to poor conditions are deposited in The Canadian Museum of Nature (CMN) in Ottawa, Ontario, Canada. The two lots at CMN are the first observations of *H. lateromaculata* outside of the type localities of Minnesota and Iowa (Mathers 1963). A specimen from Michigan was utilized in a leech phylogenetic studies (Borda and Siddall 2004).

The reproductive organs of *Haemopsis marmorata* and *H. lateromaculata* specimens collected from western North America examined are presented in this paper. Based on accurate diagnosis of the species, the external characteristics (pigmentation patterns) were

determined to distinguish these two species from one another. The results herein describe the geographical distribution of *H. lateromaculata*, and support some taxonomic and paleogeographic hypotheses concerning the family Haemopidae.

Methods

Specimens of *Haemopsis* were collected during the last 20 years from localities in western North America. The surveys consisted of visual encounters and hand picking from the underside of stones, logs, and aquatic vegetation. The specimens were relaxed with 10% ethanol, blotted by paper towel to removed the mucous excreted from the relaxation process, fixed with 10% formalin in phosphate buffered saline between two sheets of paper towels overnight, and placed in 70% ethanol for preservation.

Identification of all large *Haemopsis* specimens was determined by examining the reproductive organs through a mid-dorsal cut from the annulus with the female gonopore posteriorly approximately 20 annuli. If the penis sheath was not located with this examination, the dorsal cut was extended anteriorly for some 10 annuli. Teeth and jaws were examined by a mid-ventral cut of the lower lip. Posterior sucker width, pigmentation, and gonopore positions were noted. Small specimens were identified by pigmentation. Identifications followed original descriptions and taxonomic keys (Mathers 1963; Klemm 1985; Sawyer and Shelley 1976).

The facilities and specimens of the United States National Museum (USNM), Washington D.C. and the Canadian Museum of Nature (CMN), Ottawa, Ontario were utilized. The western specimens of Haemopidae in these collections were confirmed by dissection if the length was greater than 40 mm, and pigmentation patterns and the presence of teeth were examined. The eastern specimens of *Haemopsis marmorata* were select-

ed by pigmentation with dissection on random samples. Specimens were also examined from water quality studies in Wyoming (Wyoming Department of Water Quality), now residing in the Albertson College of Idaho Orma J. Smith Museum of Natural History (ALBRCIDA), Boise, Idaho.

Taxonomic status

There is presently full acceptance of the haemopisine species (Davies 1991; Klemm 1985; Sawyer 1986). The higher classification of leech groupings, and leeches within the Annelida, is presently contentious, however. Historically, all the haemopisine species were placed in the genus *Haemopsis* including the original description by Mathers (1954, 1963) of *H. kingi* Mathers 1954 and *H. lateromaculata*. Richardson (1969) revised the family Hirudinidae, established the family Haemopidae, and revised the genus classification by introducing the genera *Percymoorensis* including *P. terrestris* (Forbes 1890), *P. marmorata*, *P. lateromaculata*, and *P. kingi*), *Mollibdella grandis*, and *Bdellarogatis plumbeus* Moore 1912). He retained *Haemopsis* for the Eurasian *H. sanguisuga* Linnaeus 1758. Richardson (1971) suggested that *Percymoorensis* and *Haemopsis* (the Eurasian species) were associated in the subfamily Haemopinae, and that *Mollibdella* and *Bdellarogatis* were in the subfamily Mollibdelinae; he also identified a Mexican species *Percymoorensis caballeri* Richardson 1971 in that paper.

Davies (1991); Davies and Govedich (2001); and Soós (1969) accepted the generic nomenclature of Richardson (1969) but retained the earlier familial classification of Hirudinidae. Soós (1969) expressed reservation about Richardson's classification of Hirudinidae (including Haemopidae) based on his use of type-specimens, and that "long standing genera are strongly heterogeneous in content and cannot any longer be separated one from the other entirely by single factors, or contained within single divisions in the key". Klemm (1995), Manoleli et al. (1998), and Sawyer (1986) rejected the generic nomenclatural changes of Richardson but accepted the family Haemopidae classification.

A new species, *Haemopsis septagon* Sawyer and Shelley 1976, was described from specimens collected from North Carolina in eastern United States. In their description Sawyer and Shelley noted that if the classification of Richardson (1969) was accepted, *H. septagon* warranted placement in a new genus. Davies (1991) placed this species with the genus *Percymoorensis*. The uncertainty of Richardson's classification with respect to *H. kingi* and *H. lateromaculata* was revealed when Richardson (1969, 1971) stated that these two species most likely belong to a new genus. He did not examine either species but relied on Mathers (1954, 1963) for his paper (Richardson 1969). Borda and Siddall (2004) examined six species of *Haemopsis* for phylogenetic studies involving anatomical characteristics, 12 S mitochondrial rDNA, 18S and 28S nuclear rDNA,

and cytochrome c oxidase subunit I gene fragments. Of the 24 anatomical criteria that were utilized, 23 were common to all six species, thus not significant in determining genera or species relations. Borda and Siddall (2004) confirmed the family Haemopidae. I maintain use of the genus *Haemopsis* and the family Haemopidae until additional and more conclusive phylogenetic studies have been reported for all the hemopisine species, using population samples representing the entire range of these widespread species.

Results

Distribution of *Haemopsis lateromaculata* in North America

The Nearctic distribution of *Haemopsis lateromaculata* is shown in Figure 1 and listed in Table 1. This distribution is based on museum specimens (USNM, ALBRCIDA, and CMN), from my (PH) collections from the geographical studies in western North America and from water quality studies in Wyoming (ALBRCIDA). Anatomical dissections distinguished *H. lateromaculata* from *H. marmorata* in western North America when the plain ventrum and plain, cream, or yellow colored lateral margins were prominent, and thus could be used to distinguish these two congeners from one another. Based on this pigmentation distinction, juvenile specimens (< 40 mm) and museum specimens in eastern North America *H. marmorata*, were examined and those with no ventral pigmentation were considered *H. lateromaculata*. Some specimens without pigmentation were dissected and the species determined. The following are the locations of *Haemopsis lateromaculata* (underlined accession numbers refer to museum specimens catalogued as *H. marmorata* or as *Haemopsis*). Most of these misidentified specimens had been catalogued and accessioned into the museum collections before the work of Mathers (1963) had been completed and published.

Alaska: USNM 19230 Yes Bay, 20732 Afognak Island, 21255 Yes Bay, 21256 Sanak Island, 43455 Revillagigedo Island, CMNA 1982-0746 Esther Island, and PH collections from Susitna River drainage, Kenai Peninsula, and Kodiak Island.

Western Canada: Yukon Territory: PH collection from Pelly River drainage (Yukon River drainage); British Columbia: USNM 19231 North Fork Moose River (at least two Moose Rivers occur in British Columbia), and USNM 38352 "D" [Dee] Lake; CMNA 1985-0289 and CMNA 1990-0056 (identified by J. Madill, but was not found in the collection) Fraser River drainage; and from PH collections from the Fraser River drainage (CMNA 2006-0036) and Haida Gwaii (Queen Charlotte Islands) (CMNA 2006-0037); Alberta: CMNA 1978-0426 Mackenzie River drainage; and from PH collection Peace River drainage (Mackenzie River drainage) (CMNA 2006-0034).

Lower western United States: Idaho: from PH collection in the Snake River drainage (Columbia River

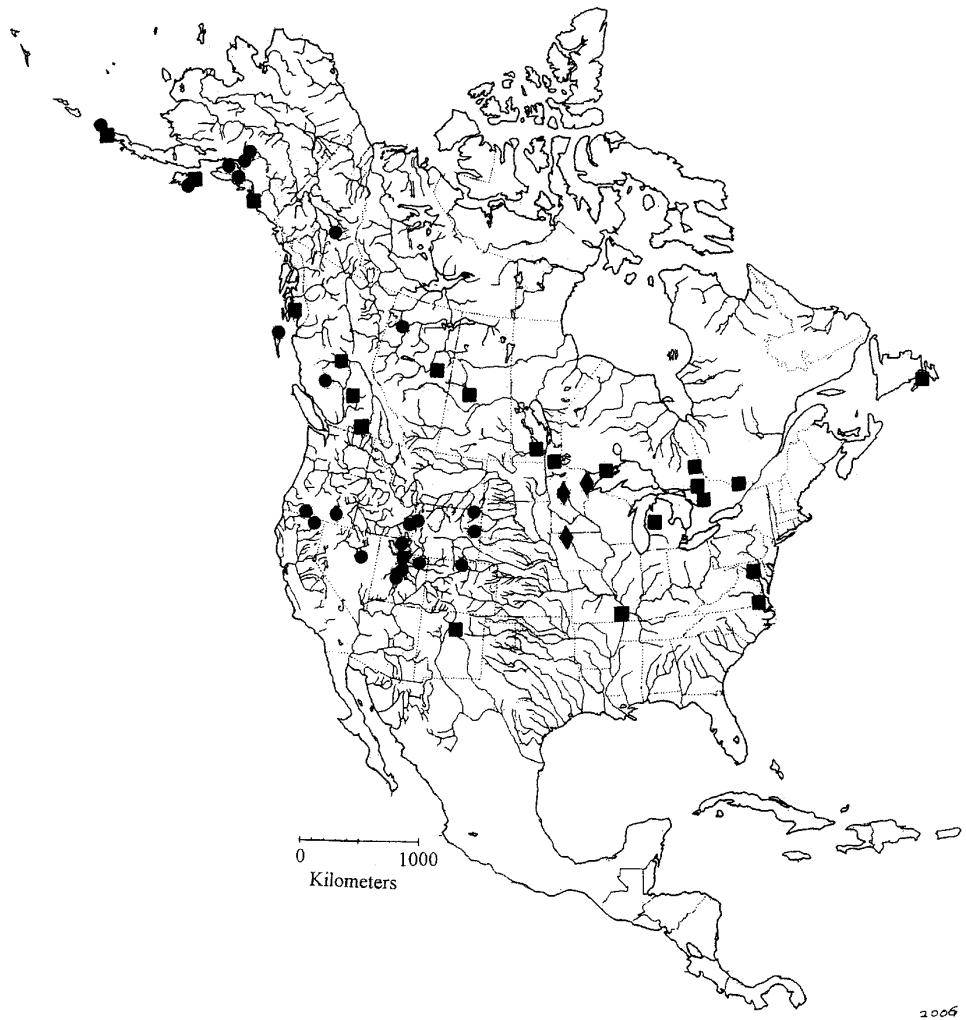


FIGURE 1. The distribution of *Haemopis lateromaculata* in North America. Locations are shown by (a) squares, museum specimens (NMNH, CMN); (b) circles, western North America survey sites (preliminary results) and identifications from Wyoming water quality studies; and (c) diamonds, Mathers (1963) locations.

drainage); Oregon: from PH collection in the Klamath River drainage and the Great Basin; Wyoming: from PH collection in the Snake River drainage (Columbia River drainage) and Water Quality Studies in Missouri River drainage (ALBRCIDA 61050-61052); California: from PH collection in the Pit River drainage (Sacramento River drainage); Nevada: from PH collection in the Great Basin; Utah: USNM 38308, 39056, USNM 38624, 38627 (the latter two identified to genus), and from PH collection in the Great Basin and Colorado River drainage; Colorado: from PH collection in the South Platte River drainage (Missouri River drainage);

New Mexico: USNM 50192 Rio Grande drainage (did not dissect).

Eastern North America: Canada: Saskatchewan: USNM 38353; Manitoba: USNM 38347, CMN 1985-0292, 1985-0301; Ontario: USNM 38360, 38348, CMN 1985-0253, 1985-259, 1985-279, 1987-0670, 1988-0036, 1988-0163; Newfoundland: CMN 1982-0654, 1985-0378 (both identified by J. Madill); lower United States: Michigan: USNM 38331; Missouri: USNM 20681; District of Columbia: USNM 30223; Virginia: USNM 42650.

TABLE 1. Distribution of *Haemopsis lateromaculata* in North America, from the field collections in western North America and from the Orma J. Smith Museum of Natural History (ALBRICIDA), Canadian Museum of Nature (CMNA), and the United States Museum of Natural History (USNM). (1) In poor condition or not found in the collection. (2) At least two Moose Rivers in British Columbia. (3) *Haemopsis* unidentified. PH, Peter Hovingh collection work in progress.

Province or State	Catalogue	Date	Locator
Alberta	CMNA 1978-0426	1907	Beaver Lake
Alberta	CMNA 2006-0034	2000	Slave River drainage
British Columbia	CMNA 1985-0289	1976	150 Mile House
British Columbia	CMNA 1990-0056	1989	Cariboo District
British Columbia	CMNA 2006-0036	1988	Chilcotin River drainage(1)
British Columbia	CMNA 2006-0037	2000	Haida Gwaii
British Columbia	USNM 19231	1911	North Fork Moose River (2)
British Columbia	USNM 38352	1935	[Dee] "D" Lake
Manitoba	CMNA 1985-0301	1970	Vita
Manitoba	CMNA 1985-0292	1976	LaSalle River
Manitoba	USNM 38347	1927	
Newfoundland	CMNA 1982-0654	1981	Placentia Bay
Newfoundland	CMNA 1985-0378	1985	St Marys Bay
Ontario	CMNA 1985-0259	1920	Abitibi River
Ontario	CMNA 1985-0262	1920	Missinaibi River
Ontario	CMNA 1985-0253	1922	Ottawa River
Ontario	CMNA 1985-0279	1965	Albany River
Ontario	CMNA 1988-0036	1987	Thunder Bay
Ontario	CMNA 1988-0163	1987	Rainy River
Ontario	CMNA 1987-0670	1987	Kenora
Ontario	USNM 38348	1925	Lake Abitibi
Ontario	USNM 38360	1931	Lake Nipissing
Saskatchewan	USNM 38353	1940	Waskasov
Yukon Territory	CMNA 2006-0035	2000	Pelly River drainage
Alaska	CMNA 1982-0746	1961	Esther Island
Alaska	CMNA 1985-0297	1961	Hinchinbrook Island (3)
Alaska	CMNA 1978-0360	1961	Chuckagof Island (3)
Alaska	USNM 19230	1905	Lake Mc Donald, Yes Bay
Alaska	USNM 21225	1907	Lake Mc Donald, Yes Bay
Alaska	USNM 20732	1938	Afognak Island
Alaska	USNM 21256	1937	Sanak Island
Alaska	USNM 43455	1897	Revillagigedo Island
Alaska	PH 1671-1677	2003	Kodiak Island
Alaska	PH 1660	1994	Cook Inlet
Alaska	PH 1661-1664	2003	Cook Inlet
Alaska	PH 1667, 1669	1994	Kenai Peninsula
Alaska	PH 1665, 1666	2003	Kenai Peninsula
Alaska	PH 1668, 1669	2003	Kenai Peninsula
Alaska	PH 2029	2006	Cold Bay, Alaska Peninsula
California	PH (0000)		Pit River
Colorado	PH (0000)	2002	Great Plains
District of Columbia	USNM 30223	1911	Easter Branch
Idaho	PH (0000)	1994	Snake River drainage
Michigan	USNM 38331	1925	Mecosta County
Missouri	USNM 20681	1935	Sikeston
Nevada	USNM (PH 848)	1989	Ruby Marsh
New Mexico	USNM 50192	1929	Pecos River
Oregon	USNM (PH 852)	1996	Catlow Valley
Oregon	PH (0000)	1995	Klamath Lake
Utah	USNM 38308	1952	Provo
Utah	USNM 38624	1952	
Utah	USNM 38627	1952	Mapleton
Utah	USNM 39056	1952	Provo
Utah	USNM (PH 497)	1990	Provo River
Utah	USNM (PH 498)	1995	Provo River
Utah	USNM (PH 499)	1989	Provo River
Utah	USNM (PH 489)	1989	Sevier River
Utah	USNM (PH 491)	1995	Sevier River
Utah	USNM (PH 487)	1990	Weber River
Utah	USNM (PH 488)	1994	Weber River
Utah	USNM (PH 486)	1993	Bear River

TABLE 1. *continued*

Province or State	Catalogue	Date	Locator
Virginia	USNM 42650	1957	Dismal Swamp
Wyoming	PH (0000)	1991	Snake River drainage
Wyoming	ALBRICIDA 61050	1994	Johnson County
Wyoming	ALBRICIDA 61051	1997	Crook County
Wyoming	ALBRICIDA 61052	1997	Niobrara County

Identification of leech specimens: external characteristics

TEETH. All of the *Haemopsis lateromaculata* contained teeth (denticles). This characteristic would separate these specimens from *H. plumbea* and *H. grandis*. Four populations (Utah, Nevada, Wyoming, Montana) of *H. marmorata* were without teeth. One population (Utah) was collected in 1941 (USNM 50195) and again in 1986 suggesting that the loss of denticles may be due to environmental or genetic factors resulting from colonization after the dessication of Lake Bonneville after 13 000 years ago.

POSTERIOR SUCKER. Although the posterior sucker is large (about $\frac{3}{4}$ the width of the body) in *Haemopsis lateromaculata* and small (less than $\frac{1}{2}$ the width of the body) in *H. marmorata* (Klemm 1985), the state of body relaxation was highly variable. This variability made the relative size of the posterior sucker to body width rather arbitrary.

PIGMENTATION. The dorsal surface of *Haemopsis lateromaculata* was patterned with darker blotches or mottled, or large to small speckles, of frequent to rare numbers. The lateral margins were cream or yellow (shared with *H. terrestris*) and interrupted with irregular dark intrusions dorsally (a very diagnostic character), visible from both the dorsal and ventral surface [specimens from 14 sites: the Great Basin (8), Colorado River drainage (2), Great Plains (1), Columbia River drainage (2), and the Yukon River drainage (1)]; or with the lateral margins the same shade as the ventrum, without cream or yellow coloring [specimens from 21 sites: the Great Basin (2), Pacific Coast drainages (2), Fraser River drainage (1), Mackenzie River drainage (1), coastal islands and their adjacent shores of British Columbia and Alaska (17)]. The external characteristic that identified all of the specimens was the plain ventral surface. Mathers (1963: page 170) noted "with a few indistinct black and yellow blotches" on the ventral surface. I observed one specimen with an occasional speckle on the ventral surface.

The pigmentation of *H. marmorata* in western North America ranged from heavily blotched or mottled to heavily speckled or lightly speckled on both the dorsum and ventrum (61 sites), with the ventrum having subdued pigmentation of the same pattern. If either *H. lateromaculata* or *H. marmorata* were of the light- and/or dark-colored immaculate phase (Klemm 1985: page 155), pigmentation could not be used to identify these two species. The light-colored immaculate phase was not found in the living state in western North America, but only in preserved specimens in museums. The lack

of a dorsal stripe excluded *H. terrestris*, *H. kingi*, and *H. septagon* from further consideration in this study.

MAXIMUM LENGTH (MM). *Haemopsis lateromaculata*: Great Basin (90), Colorado River drainage (67), Columbia River drainage (31), Mackenzie River drainage (83), Fraser River drainage (30), Queen Charlotte Islands (81), Yukon River drainage (82), Alaska (112), and Great Plains (50). *Haemopsis marmorata*: Great Basin (112), Colorado River drainage (95), Columbia River drainage (121), Pacific Coast drainages (98), Fraser River drainage (98), and Great Plains (94). Length is highly variable, dependent upon both the age of living specimens and their state of relaxation during fixation.

GONOPORE POSITIONS. *Haemopsis lateromaculata*: Male gonopore XI *b6* anterior $\frac{1}{2}$; female gonopore XII *b6* anterior $\frac{1}{2}$, as determined on two specimens with developed clitellum from Nevada and Yukon Territory. All gonopore positions were separated by 5 annuli and occurred on the anterior $\frac{1}{2}$ of the annulus. *Haemopsis marmorata*: Male gonopore XI *b6* anterior $\frac{1}{2}$; female gonopore XII *b6* anterior $\frac{1}{2}$, as determined on three specimens with developed clitellum from Nevada and Colorado. Most gonopore positions were separated by 5 annuli and occurred on the anterior $\frac{1}{2}$ of the annulus. Three exceptions: male XI *b6* mid-annulus and female XII *b6* mid-annulus, and male XI *b6* mid-annulus and female XII *b5* posterior $\frac{1}{2}$ both from Arizona; and male and female on mid-annulus from British Columbia. Sawyer (1972) noted additional variations of the gonopores from mid-annulus to the furrow. The male and female gonopore separations excluded *H. septagon* from further consideration during this study.

Identification of leech specimens by reproductive organs

Figure 2 illustrates the mean measurements of the reproductive organ position and Table 2 lists the mean \pm standard deviation. The posterior position of the left and right ejaculatory bulbs, the posterior position of the penis sheath loop and the vagina organs, and the anterior position of the prostate organ (anterior end of male atrium) were selected for their defined shape, largely attributed to the muscular nature of the organs (Richardson 1969). The organ positions were determined by vertical positioning of the organ with the annulus, and hence counting the number of annuli to the annulus with the female gonopore. There is a possible error of annuli count of ± 1 annulus due to the positioning in individual specimens. The nomenclature of the organs follows that of Klemm (1985). Left and right positions are determined from the dorsal side. Comparison to

other species is based on literature (Klemm 1985; Mann 1954; Richardson 1971).

PENIS SHEATH LOOP. *Haemopsis lateromaculata*: The penis sheath loop was located at annulus XIII b5 (XII b6 to XIV a2). The penis sheath was generally U-shaped and distinguished *H. lateromaculata* from *H. marmorata*, *H. plumbea*, *H. terrestris*, *H. septagon*, and *H. caballeroi*. *Haemopsis marmorata*: The penis sheath loop was located at annulus XVII b1 (XVb1 to XVIII b5), a range comparable to Sawyer (1972). The penis sheath was generally J-shaped and on the left side. The ranges did not overlap between *H. lateromaculata* and *H. marmorata*. The average length of the penis sheath of *H. lateromaculata* was 21 annuli and of *H. marmorata* 38 annuli between the male gonopore and the prostate gland. Abnormal variations for the penis sheath of *H. lateromaculata* include position on the right side (4 specimens from Yukon Territory, Alaska, and Colorado) and highly contorted (1 specimen from Alaska). Abnormal variations for the penis sheath of *H. marmorata* include: positioned on the right side (11 specimens from Great Basin, Colorado River Basin, and Great Plains), and highly contorted (6 specimens from Great Basin, Great Plains) with one specimen in which the terminal loop turns medially and is twisted to form a topless "8".

PROSTATE GLAND. *Haemopsis lateromaculata*: The anterior end of the male atrium is covered by the prostate gland and was located at annulus XI a2 (X a2 to XII b6), positions that are anterior to the female gonopore and for the most part anterior to the male gonopore. These locations are associated with the U-shaped penis sheath. *Haemopsis marmorata*: The anterior end of the prostate gland was located at annulus XIV b5 (XIII b1 to XVI b5), defining the J-shaped penis sheath.

EJACULATORY BULBS. *Haemopsis lateromaculata*: The posterior end of the left ejaculatory bulb (seminal vesicle) was located at annulus XIII b2 (XII b2 to XIV

a2) whereas the posterior end of the right ejaculatory bulb was at annulus XIII b1 (XII b1 to XIV a2). Although the locations show left-right symmetry (Figure 2), large variations were found in which the left bulb was 10 annuli posterior to 7 annuli anterior of the right bulb. The distribution of the positions of the ejaculatory bulbs was: right anterior to the left, 13 specimens; right even with the left, 13 specimens; and right posterior to the left, 8 specimens. *Haemopsis marmorata*: The posterior end of the left ejaculatory bulb was located at XIV b2 (XIII b1 to XV b5) whereas the posterior end of the right ejaculatory bulb was at annulus XIV b1 (XII a2 to XV b6). The left bulb ranged from 9 annuli posterior to 5 annuli anterior of the right bulb. The distribution of the ejaculatory bulbs was: right anterior to the left, 19 specimens; right even with the left, 16 specimens; and right posterior to the left, 17 specimens, a pattern noted by Sawyer (1972). Two specimens had only one ejaculatory bulb.

VAGINA. *Haemopsis lateromaculata*: The posterior end of the vagina (vaginal bulb) was found at XIV b6 (XIII a2 to XVII a2). The vagina was always posterior to the posterior reach of the penis sheath loop and was generally in the median region. *Haemopsis marmorata*: the posterior end of the vagina was found at XVI b1 (XIV b2 to XVII a2), comparable to the findings of Sawyer (1972). The vagina was always anterior to the posterior reach of the penis sheath loop and posterior to the anterior end of the prostate gland, and generally located in the medial region. Three specimens had the vagina location anterior to the anterior end of the prostate gland. The position of the vagina of *H. caballeroi* had a relative position to the penis sheath loop and the prostate gland (atrium) as in *H. marmorata*, but the two specimens of *H. caballeroi* were highly contracted and hence not typical (Richardson 1971). The extensive penis sheath and its relation to the vagina suggests that these two species deserve a separate genus — in

TABLE 2. Annuli location of selected reproductive organs in *Haemopsis marmorata* and *H. lateromaculata*. Annulus X b1 was number 1 and annuli posterior to this annulus were sequentially numbered. Organ nomenclature was taken from Klemm (1985). Figure 2 illustrates the organs and the points of measurement.

	<i>H. lateromaculata</i> N = 31	<i>H. marmorata</i> N = 55
Penis sheath loop		
Mean ± standard deviation	18.8 ± 2.6	35.8 ± 4.6
Range	14 – 23	25 – 44
Anterior prostate gland		
Mean ± standard deviation	7.2 ± 2.5	23.9 ± 3.7
Range	2 – 14	16 – 35
Posterior left ejaculatory bulb		
Mean ± standard deviation	16.7 ± 3.0	21.3 ± 3.4
Range	11 – 23	15 – 29
Posterior right ejaculatory bulb		
Mean ± standard deviation	15.5 ± 3.1	21.0 ± 3.4
Range	10 – 23	12 – 30
Posterior vagina		
Mean ± standard deviation	24.6 ± 4.7	30.5 ± 3.7
Range	17 – 38	21 – 38

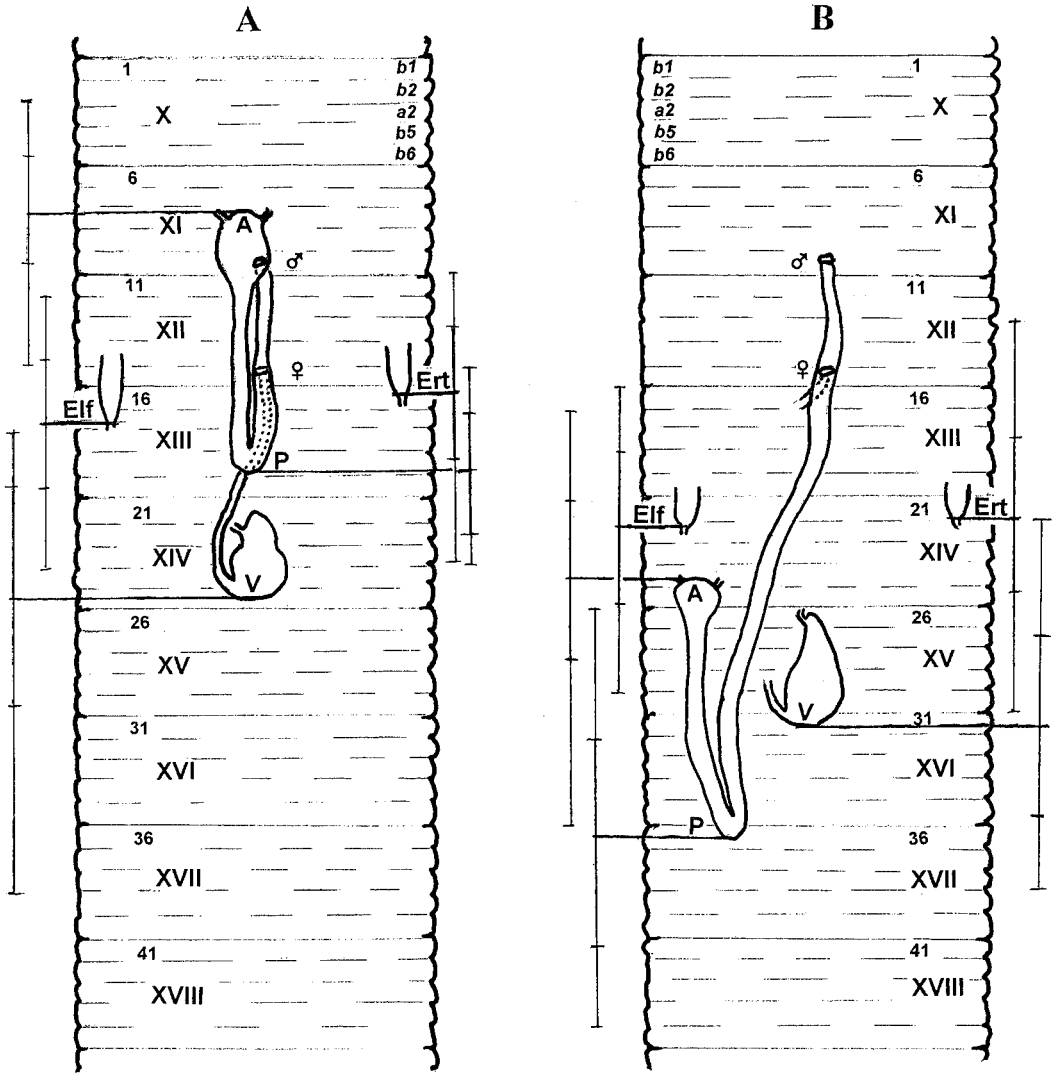


FIGURE 2. Measured reproductive organs in *Haemopsis lateromaculata* (A) and *H. marmorata* (B), viewed from the dorsum. The segments are shown in Roman numerals starting with segment X and extend to segment XVIII. Each segment has five annuli as denotated names shown on the right side of segment X. For the purposes of this paper, the first annulus is numbered 1 and is sequenced posteriorly as noted on the left side with only the first annulus of each segment numbered (see Table 2). Male gonopore on IX b6 and female gonopore on XII b6. Denotations: Elf, posterior reach of the left ejaculatory bulb; Ert, posterior reach of the right ejaculatory bulb; P, posterior reach of the penis sheath loop; V, posterior reach of the vagina; and A, the prostate gland at the anterior end of the male atrium. The vertical lines represent one standard deviation (thick lines) and total range (thin lines) (see Table 2).

this case *Percymoorensis*, if one follows the distinct genera classification in Erpobdellidae of *Nephelopsis*, *Mooreobdella*, and *Erpobdella*, each having morphological distinct male atriums and sperm ducts.

Discussion

Haemopsis lateromaculata is now considered to be widely distributed throughout North America; prior

to this study, its known distribution had been limited to two states (Figure 1). The presence of this leech on the Alaskan Peninsula and adjacent islands, the Cook Inlet region, the Alexander Archipelago of southeast Alaska, and Haida Gwaii (Queen Charlotte Islands) of British Columbia suggest that these leeches occupied off-shore coastal refugia during the Pleistocene and were separated from those populations south of Canada's cordil-

leran and continental glaciers. These northwest refugia were limited by extensive glaciers from Haida Gwaii to Umnak Islands (Coulter et al. 1965; Clague 1989; Kaufman and Manley 2004) with coastal cordilleran glaciers occurring to 12 000 years ago (Peltier 1994; Dyke 2004; Fulton et al. 2004). While the occurrence of small terrestrial refugia have been postulated from Kodiak to the Queen Charlotte Islands (Heusser 1989; Ramsey et al. 2004), present day freshwater habitats (ponds, lakes, slow moving and meandering streams) from which leeches have been collected add a new dimension to the terrestrial refugia.

The Pleistocene-Holocene environments were changing due to eustasy (the sea level rising at least 120 m) and glacio-isostatic surface adjustments involving the advance and recession of the glaciers. Hetherington et al. (2003, 2004) mapped this environment for the Haida Gwaii and described a land bridge between the islands and the British Columbia mainland that existed between 11 700 and 11 200 years ago as a result of the presence of a forebulge from the retreating cordilleran glacier. This process, if applied throughout the glaciated region of coastal Alaska, may have allowed island by island transfer of leeches from coastal Pleistocene refugia, thus accounting for the modern day presence of *H. lateromaculata* populations on the coastal northwestern North America mainland (Reimchen and Byun 2005). Upstream movement of *H. marmorata* has been noted (Herrmann 1970; Richardson 1942; Sawyer 1970), and active movement (to Prince Edward Island) must have occurred by direct means, and not as passive movement by birds or other agents (Richardson 1943). It is assumed herein the cordilleran glaciers and marine habitats prevented any leeches from continental populations colonizing the coastal habitats.

Lukin (1976) suggested that *Haemopsis* originated in the Nearctic and penetrated the Palaearctic from the northeast [Siberia] when northern Asia had a warmer climate. He further suggested that *H. sanguisuga* emerged at that time and is now found across central Eurasia to the Amur Basin and near Vladivostok in eastern Asia, but not in Kamchatka Peninsula. The center of biodiversity of *Haemopsis* is in eastern North America, supporting Lukin's postulate. Only two species (*H. lateromaculata* and *H. marmorata*) moved out of this region to occupy most of North America, and only *H. lateromaculata* has been identified in Alaska and the coastal islands, suggesting range expansion in an earlier epoch before the range expansion of *H. marmorata*. From the Late Cretaceous (80 million years ago) to the middle Pliocene (3 million years ago), North America and eastern Asia were connected between Alaska and eastern Siberia (Repenning and Brouwers 1992; Smith et al. 1994). For much of this time, the climate in this region was comparable to that of the southeastern United States today (Bassinger 1991).

I propose that *H. lateromaculata* and *H. sanguisuga* are sister species. Two anatomical features of *H. lat-*

eromaculata and *H. sanguisuga* support this relationship: (1) the vaginal bulb lies posterior to the penis sheath loop (shared with *H. grandis* and *H. kingi*) and (2) the prostate gland (anterior end of the male atrium) occurs mostly anterior to the male gonopore (shared with *H. kingi* and *H. caeca*) (Mann 1954; Klemm 1985; Manoleli et al. 1998). Note that *H. kingi* occurs in both groups, a confirmation of Richardson's (1969, 1971) views that *H. kingi* and *H. lateromaculata* are closely related.

The distribution of a species is as important as the original description of a species. As noted by Newton (2003: page 90) with respect to birds, "how species are formed is central to understanding their distributions" and "genealogy and distribution are not separate issues: they are simply different sides of the same biological coin". This paper contributes to the definition of *H. lateromaculata* by the addition of geographical limits of its distribution and its evolutionary implications.

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