Terrestrial gastropods from Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada, including description of a new northern endemic slug (Gastropoda: Stylommatophora: Arionidae)

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ABSTRACT

Reflecting its isolation, geography, and glacial history, the Haida Gwaii archipelago (Queen Charlotte Islands, British Columbia) contains numerous endemic and disjunct taxa of various groups of organisms, but terrestrial gastropods have received scant attention. During surveys of 56 sites on Graham and Moresby Islands and 11 smaller islands, including remote mountain top locations, we detected 18 species of native terrestrial gastropods, most of which also occur in southwestern British Columbia. An undescribed species of semi-slug was found at four sites on Graham Island and six sites on Moresby Island and is formally described (Arionidae: *Staala gwaii*). Morphological and anatomical analyses suggest that the new slug is related to small species of *Hemphillia* Bland and Binney, 1872, but the differences are substantial, warranting the establishment of a new genus. The new species is of particular interest because it appears to be a northern endemic and a relict to the archipelago.

Additional keywords: Gastropoda, Arionidae, *Staala gwaii*, Queen Charlotte Islands, anatomy, endemism

INTRODUCTION

Haida Gwaii (Queen Charlotte Islands) is an isolated archipelago located at the edge of the North American continental shelf in the North Pacific Ocean. A distance of at least 80 km separates the islands from the nearest landmass to the east across Hecate Strait on the mainland British Columbia and to the north across Dixon Entrance on the Alaskan panhandle. The biota of the islands includes endemic and unusual disjunct populations from a wide range of taxonomic groups (e.g., vascular plants: Ogilvie, 1989, 1994; bryophytes: Schofield, 1989a,b; carabid beetles: Clarke et al., 2001; birds and mammals: McTaggart Cowan, 1989). Endemism and disjunct distributions have been interpreted to reflect the geographic isolation of the archipelago and differentiation *in situ*, in combination with complex patterns of past recolonization and extinction events.

Terrestrial gastropods of Haida Gwaii are poorly documented, and knowledge of this group is largely restricted to serendipitous observations as part of studies of other organisms. Terrestrial gastropods as a group can be useful for elucidating phylogeographic patterns, as many species have poor dispersal abilities if not aided by humans and can survive in small habitat patches (Cowie and Holland, 2006). From 2000 to 2004, we surveyed numerous sites on the two main islands (Graham and Moresby) and on smaller islands of the archipelago for terrestrial gastropods. Here we report the results of these surveys and describe a new genus and species of arionid semi-slug, presumed to be a relict, and endemic to the archipelago.

MATERIALS AND METHODS

Study Sites: We sampled 56 sites on Graham (6883 km^2) and Moresby (3066 km^2) islands and on 11 smaller islands in the Hecate Strait: Lyell (181 km^2), Kunghit (134 km^2), Burnaby (66 km^2), Tanu (23 km^2), Huxley (6.7 km^2), SGang Gwaii (2.9 km^2), Kat (0.7 km^2), Bischofs (1.1 km^2), Hotspring (0.2 km^2), Ellen (0.2 km^2), and Slug Islet (0.03 km^2) (Figure 1; see RBCM website for coordinates and habitat descriptions). More than one habitat or sub-site within a 1 km area was sampled at seven of these sites. The surveys took place in Apr. 2000, Jul.–Oct. 2002, Sep.–Nov. 2003, and Sep. 2004. The focus was on old-growth forest (28 sites), dominated by *Picea sitchensis*, *Tsuga heterophylla*, and *Thuja plicata* and with an understory of *Vaccinium* species, *Gaultheria shallon*, *Menziesia ferruginea*, and *Blechnum spicant*. Other habitats sampled consisted of older (> 80 years old) second-growth coniferous forest (12 sites), young forest with a large component of *Alnus rugosa* (< 60 years old) (3 sites), subalpine and alpine meadows (7 sites), bog

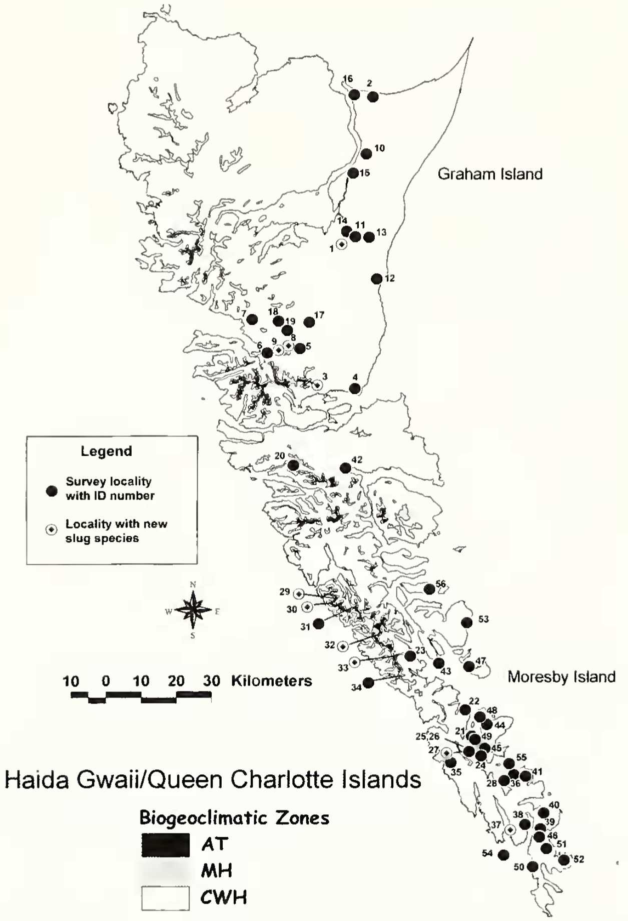


Figure 1. Map of sampling sites in the Haida Gwaii (Queen Charlotte Islands archipelago. Site numbers correspond to those in Table 1 (see RBCM website for coordinates and habitats). Biogeoclimatic zones: AT-alpine tundra, MH-mountain hemlock, CWH-coastal western hemlock (Meidinger and Pojar, 1991).

with stunted trees (3 sites), and other open habitats (rocky bluff, wet meadow, riparian fringe, thermal meadow, sand dune) (9 sites). The alpine sites were on rocky slopes with sparse ground cover, including hummocks of grasses, sedges, heathers, and crowberry (*Empetrum nigrum*). The subalpine sites contained scattered stunted trees and shrubs, including *Pinus contorta*, *Chamaecyparis nootkatensis*, *Tsuga mertensiana*, and *Juniperus* species. In 2004, we specifically targeted subalpine-alpine habitats, which were suspected to support populations of the new species of slug.

Gastropod Sampling and Identification: The main survey methods consisted of timed searches of natural cover on the forest floor (59 plots at 50 sites) and inspections of cardboard cover-objects (36 plots at 9 sites). Additionally, we extracted small snails from litter samples from two sites, including an experimental forestry site that was sampled intensively in two years (102 l of litter dried and sieved and residues examined for snail shells). Searches of natural cover focused on key microhabitat features for gastropods, such as piles of bark or an abundance of decaying logs or stumps. Observers visually scanned the surface of the forest floor and vegetation, turned over downed logs, sloughed-off bark, and rocks, and examined handfuls of leaf-litter. At one site (Site 2a–d in Figure 1), the surveys were both time- and area-constrained, and the observers searched 100×1 m transects in four different habitats for 40 minutes. The total search time for surveys of natural cover was 86.7 person-hours ($\bar{x} \pm SE = 88 \pm 7$ min/site).

The cardboard cover-object method (Hawkins et al., 1998) permitted repeated sampling of gastropods with minimal disturbance to the habitat. We used cover-objects constructed of layers of corrugated cardboard (dimensions 30 cm x 30 cm) placed at stations 10 m apart along transects of 10 sampling stations and inspected them one or more times after they had weathered on the forest floor for at least two weeks. There were a total of 1072 cardboard cover-objects on 36 plots at 9 sites. One site (Site 1 in Figure 1) was used as an experimental site for investigating logging effects and was sampled intensively and repeatedly (800 cover-objects inspected four times; in 2002 and 2006; KO and LS, unpublished data).

Identification of gastropods was based on descriptions in Pilsbry (1940, 1948) and Forsyth (2004). Nomenclature follows Forsyth (2004). Snails were identified using shell characteristics. Any small snails that could not be readily identified in the field were collected and examined under a dissecting microscope. Some snails (notably juveniles of *Ancotrema* and *Pristiloma*, and most *Vertigo*) were identified to genus only. Of slugs, several specimens of *Staala gwaii*, new species, and a sample of *Prophysaon foliolatum*, and *P. vanattae*, were dissected, and their reproductive anatomy was examined. Voucher specimens are deposited in the Royal British Columbia Museum, Victoria, British Columbia, Carnegie Museum of Natural History, and in the personal collections of K. Ovaska and R. Forsyth.

Dissection of Specimens: Seven specimens of the new species, preserved in 70% ethanol, were dissected by LC under a dissecting microscope (7.5–35X magnification). Parts removed for further study were mounted on standard microscope slides and examined under a compound microscope (40–400X magnification). Hematoxylin stain was used to make a permanent slide of the penis. Mounted specimens were dehydrated in 95% and 100% ethanol. Toluene was used as a clearing agent and specimens were mounted in Permount (Fisher Scientific, Fairlawn, New Jersey).

RESULTS

Gastropod Species Found

Surveys of 56 sites resulted in the detection of 18 native and four alien species of terrestrial gastropods (Table 1). Five species predominated in the samples: *Ariolimax columbianus* (71.4% of sites), *Vespericola columbianus*

Table 1. Species of terrestrial gastropods by locality found during surveys in Haida Gwaii (Queen Charlotte Islands) in 1999 – 2004. See Figure 1 for location of the sites, indicated by numbers (letters denote sub-sites).

Species	Graham Island (n = 19 sites)	Moresby Island (n = 23 sites)	Small outer islands (n = 14 sites on 11 islands)
Agriolimacidae:			
Deroceras laeve Müller, 1774	2a, 5, 17	26	
Deroceras reticulatum Müller, 1774*	2d		47b
Arionidae:			
Ariolimax columbianus Gould *in* A. Binney, 1851	1, 2b–d, 3a, 4, 5, 6, 7, 11, 12, 13, 14, 15, 16b, 17, 18	20, 21, 22, 24, 25, 27c, 28, 29, 30, 37, 38, 39, 40, 41, 42	43, 45a, 46, 47b, 48, 50, 53, 54a,b, 55, 56
Arion rufus Linnaeus, 1758*	2d, 4		
Arion subfuscus Draparnaud, 1805*	2d, 16a	36	
Prophysaon foliolatum Gould *in* A. Binney, 1851	1, 2a–d, 4, 5, 6, 7, 9, 12, 13, 14, 15, 16b, 17	23, 27c, 30, 31, 33, 34, 35, 36, 40, 41	43, 45b, 46, 47b, 48, 50, 51, 52, 53, 54a, 56
Prophysaon vanattae Pilsbry, 1948	1, 2b,c, 5, 12, 14	20, 29, 30, 37	48, 52
Staala gwaii (new genus and species)	1, 3a,d, 8, 9	27b,c, 29, 30, 32, 33, 37	
Daudebardiidae:			
Nesovitrea binneyana Morse, 1864	2d		47a
Oxychilus alliarius J.S. Miller 1822*	2d		
Euconulidae:			
Euconulus fulvus Műller, 1774	1		47a
Gastrodontidae:			
Striatura pugetensis Dall, 1895	1, 2a–c, 3a, 5, 6, 12, 13	28	
Haplotrematidae:			
Ancotrema hybridum Ancey, 1888	1, 2a		51, 54a
Ancotrema Baker, 1931 sp.	6, 7, 8	39	46, 48, 53
Haplotrema vancouverense, I. Lea, 1839	1, 2a–d, 3a, 4, 5, 7, 10, 12, 13, 15, 16b, 17	20, 21, 22, 23, 24, 25, 27b, 28, 29, 36, 37, 39, 40, 41, 42	43, 44, 45b, 46, 51, 52, 53, 54a, 55, 56
Punctidae:			
Punctum randolphii Dall, 1895	1, 2a–c, 5, 6, 12	21, 23, 25, 28, 37, 41	45a, 48, 49, 50, 51, 52
Pristilomatidae:			
Pristiloma lansingi Bland, 1875	1, 4, 5, 6, 17		
Pristiloma stearnsii Bland, 1875	1, 2b,c, 3a,b, 5, 8, 9, 10, 11, 12, 19	20, 21, 22, 23, 24, 25, 28, 29, 37, 39, 40, 41	43, 44, 46, 47b, 48, 49, 50, 51, 53, 54a,b
Pristiloma Ancey, 1887 sp.(subgenus *Pristiloma*)	1, 2b,c, 3a, 4, 5, 7, 9, 11, 12	22, 28, 37, 38, 39, 40, 41, 42	48, 49, 50, 51, 52, 54a
Polygyridae:			
Cryptomastix germana Gould *in* A. Binney, 1851	1, 17		
Vespericola columbianus I. Lea 1839	1, 2a–d, 3a, 4, 5, 6, 7, 9, 10, 12, 13, 15, 18, 19	20, 21, 22, 23, 24, 25, 26, 28, 37, 38, 39, 40, 41, 42	43, 44, 45a,b, 46, 47a,b, 49, 50, 51, 52, 53, 54a,b, 56
Vallonidae:			
Planogyra clappi Pilsbry, 1898	6, 12, 18	41	
Vertiginidae:			
Columella edentula Draparnaud, 1805^	1, 8	21, 28	
Vertigo columbiana Pilsbry *and* Vanatta, 1900	1, 2b,c, 5, 6	20, 23, 25, 28	43, 48, 54b
Vertigo Müller, 1774 sp.	1, 2b,d, 8, 12	21, 22, 41	47a, 49, 50, 51, 52, 54a

*Denotes introduced species of European origin

^*Columella simplex* by some authors, in reference to the North America form of the holarctic species

(71.4% of sites), *Prophysaon foliolatum* (60.7% of sites), *Haplotrema vancouverense* (66.1% of sites), and *Pristiloma stearnsii* (57.1% of sites). All these species were widely distributed in forests throughout the archipelago. Several snails with unusual, clear, transparent shells were found at one locality on Graham Island (Site 1 in Figure 1), but were attributed to *Pristiloma stearnsii* based on other shell features.

We found 18 species of terrestrial gastropods on Graham Island and 15 on Moresby Island. On the smallest island sampled, a rocky bluff (Slug Islet), we found two species; on the remaining 10 small islands we found 4–9 species each ($\bar{x}$ = 6.4, SD = 1.6).

Alien gastropods, represented by four species, were found only at a few sites that were either disturbed and in early successional stages on Graham and Moresby Islands or received regular human visitation (Hotspring Island); older forest and small islands, apart from Hotspring Island, appeared to be free of alien species.

Slugs, represented by *P. foliolatum*, *P. vanattae*, and *S. gwaii*, dominated the gastropod fauna in the subalpine and alpine sites sampled, whereas other gastropods, including *A. columbianus*, *H. vancouverense*, and *P. stearnsii* were found infrequently and in very low numbers in these habitats; *A. columbianus* occurred only at sites with patches of trees and shrubs. *P. foliolatum* was the only gastropod found at two alpine sites that were devoid of trees and shrubs (Sites 31 and 34 in Figure1).

A New Species of Arionid Slug

A slug that did not fit within the description of any known species was encountered at four sites on Graham Island and six sites on Moresby Island (Figure 2, 3). The localities were near Rennell Sound, south of Port Clements, and on Mt. Genevieve (Sleeping Beauty Massif) on Graham Island, and on Yatza Mountain, Mt. Oliver, Mt. De la Touche, unnamed mountains near Sunday Inlet and Kostan Inlet, and in Louscoone Inlet on Moresby Island.

Superficially, the slug resembled *Hemphillia glandulosa* Bland and W.G. Binney, 1872, found on Vancouver Island, British Columbia, and in Washington and Oregon, but detailed morphological and anatomical examination revealed substantial differences, warranting the establishment of a new genus. Preliminary genetic analyses using mitochondrial markers also place the species apart from all known genera of arionid slugs in western North America (Clade C in Wilke, 2004: fig. 2).

Arionid genera native to the Pacific Northwest include *Zacoleus* Pilsbry, 1903, *Udosarx* Webb, 1954, *Prophysaon* Bland and W.G. Binney 1873, *Kootenaia* Leonard, Chichester and Baugh, 2003, and *Hemphillia* Bland and W.G. Binney 1872. Arionid genera share a ribbed jaw. The new slug possesses a jaw that is subdivided into sectors by evenly spaced, finely incised lines. We consider this jaw to be sufficiently similar to the jaws of other arionids to warrant the inclusion of the new species to this family. The new slug further differs from the first four genera by possessing a visceral cavity that is elevated

Figures 2–3. *Staala gwaii*. **2.** Adult (17 mm in extended length) from near Port Clements, Graham Island (Type locality, Site 1 in Figure 1). **3.** Juvenile (2 mm in extended length) from near Port Clements, Graham Island (Type locality, Site 1 in Figure 1).

into a hump and that fails to extend to the tip of the tail. It shares this character with *Hemphillia* (jumping-slugs), the only other genus of native semi-slugs known from North America. It differs from *Hemphillia* by having a shell plate that is calcareous and completely covered by the mantle and by a pattern of papillae covering the entire body. See Table 2 for comparisons of major features among western North American genera of arionids. A formal description of the new genus, *Staala*, and species, *S. gwaii*, follows.

Staala new genus

Type Species: *Staala gwaii* new species (below).

Diagnosis: Distinct from any other known arionid genus externally by having viscera in a pronounced hump and shell covered by mantle, and internally by the complexity of the penial stimulatory apparatus (see description in the following species account) and by the presence of an atrial accessory sac.

Etymology: The generic name means "slug" in Haida language and honors the aboriginal heritage of the archipelago of Haida Gwaii (Queen Charlotte Islands).

Table 2. Comparison of external and internal characteristics of *Staala* (new genus) with those of five other genera of Arionidae native to western North America.

Characteristic	*Staala*	*Zacoleus*	*Udosarx*	*Prophysaon*	*Kootenaia*	*Hemphillia*
External:						
Shell completely covered by mantle	yes	yes	yes	yes	yes	no
Shell shape	convex	convex	convex	flat	convex	convex
Shell calcareous	yes	yes	yes	yes	yes	no
Caudal mucus pore present	yes	no	no	no	no	yes
Caudal abscission line present	no	no	no	yes	no	no
Tail compressed *and* dorsally keeled	no	yes	yes	no	no	yes
Viscera in pronounced hump	yes	no	no	no	no	yes
Fleshy "horn" or protuberance on tail	yes	no	no	no	no	In many species
Internal:						
Penis reduced to a penial loop	no	no	no	yes	yes	no
Distinct epiphallus present	yes	yes	yes	yes	no	yes
Buccal *and* tentacular retractors converge	yes*	yes	yes	no	no	yes
Penial retractor present	yes	no	yes	no	yes	yes

*Except the main branch of the left tentacular retractor, which originates on the floor of the body cavity.

Staala gwaii new species

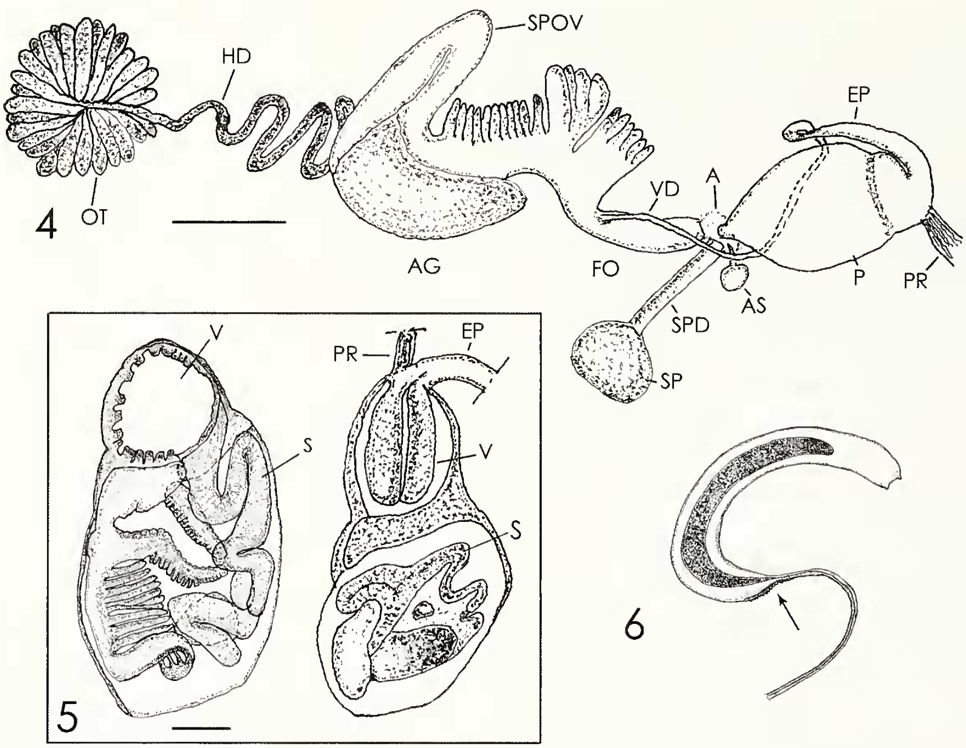
Description: Size: Very small; length of 16 live specimens was 2–17 mm ($\bar{x}$ = 9.8 mm, SD = 5.7 mm) when extended in movement. Length of 12 preserved specimens was 3–11 mm ($\bar{x}$ = 8.1 mm, SD = 2.7 mm); the difference in size between live and preserved specimens probably reflects preservation techniques (live animals were maximally extended whereas the preservative, ethanol, resulted in shrinkage). Holotype: 16 mm live, 9.4 mm preserved. Smallest dissected and preserved individuals with a mature reproductive system were 8 mm in length.

External Anatomy: The following description is based on examination of 40 individuals from ten sites and apply to the holotype, unless otherwise mentioned. Shell dome-shaped and completely covered by mantle. Outer layer horny and thin, and covering the entire visceral hump; inner layer calcareous, thickest at the center of the dome and largely absent at the margins. Mantle elliptical and large, about 2/3 the length of the body and covering the visceral pouch, which is elevated into a pronounced hump; mantle hump flattened dorsally towards its distal end and can be slightly asymmetrical, giving it a misshapen appearance. Pneumostome slightly anterior or in the middle of the right side of the mantle, near mantle margin. Tail rounded dorsally, no keel evident; tail flattened and depressed at its base where the distal portion of the mantle rests. Several elevated lines of papillae and associated grooves radiate outwards from the depression. Tail protrudes distally over foot. Caudal mucus pore present. Head, mantle, and tail covered with numerous papillae. Foot fringe moderately wide; sole undivided.

Color: Head and base of tentacles dark grey, sometimes bluish; tentacles lighter grey towards tips. Mantle mottled with dark grey and light grey (as in holotype) or tan, sometimes flecked with small tan specks. Dorsal surface of head and tail dark grey. Foot fringe light grey or tan, lighter than sides, sometimes with indistinct dark, vertical lines. Underside of head similarly light grey or tan. Black-tipped papillae often form dotted line at foot margin. Sole light grey or tan, dark grey in some melanistic individuals. Papillae covering head, mantle, and tail are light grey and black-tipped. Individuals from some localities, especially subalpine habitats on Moresby Island, were melanistic and almost uniformily dark with the exception of the sole that is slightly lighter.

Internal Anatomy: Reproductive System: The ovotestis comprises a large number of lobules (more than three dozen). It is partially embedded on the right posterior of the digestive gland. The exposed portion is lightly to moderately pigmented with black flecks. The hermaphroditic duct is long, slender, and straight in immature individuals and swollen and highly convoluted in sexually mature animals. The albumen gland is adherent to the spermoviduct (common duct). In sexually mature individuals both the albumen gland and the spermoviduct become greatly enlarged and the latter becomes structurally more elaborate. In most individuals the spermathecal duct and free oviduct enter the shallow atrium separately. In two sexually immature individuals the two ducts joined just before entering the atrium. The spermatheca (seminal receptacle or bursa copulatrix) is conical to ovoidal in shape; its duct is slender and tapered. In one specimen containing a single spermatophore, the spermatheca was forced into a fusiform shape and its duct into a corkscrew. The vas deferens arises as a slender duct from the spermoviduct, which also gives rise to the free oviduct. The vas deferens becomes even more slender as it curves around the base of the penis at the penial junction with the atrium, only to thicken again as it transitions along the side of the penis eventually to become a greatly thickened epiphallus (Figure 4).

The epiphallus enters the penis at its apex. Inserted at the apex, at this epiphallus-penis junction, is the penis



Figures 4–6. Reproductive anatomy of *Staala gwaii* (specimen from type locality). **4.** Reproductive system. **5.** Bisected penis of two specimens of *Staala gwaii* from the type locality. Left: upper verge chamber (empty) and lower stimulatory chamber with its complex folds and lobes. Scale bar = 0.2 mm; Right: bisected verge in the upper chamber and a portion of the stimulator in the lower chamber. **6.** Spermatophore (ca. 2 mm in length) showing the denticle region (arrow). Terminal portion of the filament is missing. Abbreviations: **A**, atrium; **AG**, albumen gland; **AS**, accessory sac; **EP**, epiphallus; **FO**, free oviduct; **HD**, hermaphroditic duct; **OT**, ovotestis; **P**, penis; **PR**, penis retractor muscle; **SP**, spermatheca (bursa copulatrix); **S**, stimulator; **SPD**, spermathecal duct; **SPOV**, spermoviduct; **V**, verge; **VD**, vas deferens.

retractor muscle, which is a wide band that passes directly back to its origin near the midline of the diaphragm. The penis is a large barrel-shaped structure divided internally into an upper verge chamber and a lower stimulator chamber (Figures 4, 5). A lightly pigmented band on the penis surface roughly corresponds to the boundary between the two inner chambers. The verge chamber contains a large conical structure we believe functions as a verge. The lumen of the epiphallus continues within the verge as a narrow passage that opens at or near the apex of the cone. The lower stimulator chamber is almost completely filled with a variety of attachments on the inner penial wall. Some are plumose while others are smooth-margined and lobed. In other slug species such structures have been referred to as stimulators and we extend that tradition in this case, although we have not been able to observe copulation to determine how this complex is employed. The penis enters the atrium independent of the spermathecal duct and the free oviduct. There is no accessory penial sac. However, there is a small atrial accessory sac present. This sac has a very slender duct, which enters the atrium independent of the other ducts. In immature individuals the sac is very small and difficult to see. A single spermatophore was found intact in one specimen. The spermatophore consists of a crescent-shaped main body and a long threadlike terminus (Figure 6). Near the junction of the two parts the surface bears a number of tiny denticles. The overall length of the spermatophore is about 2 mm.

Buccal and Tentacular Retractor Muscles: The left and right buccal retractor muscles fuse just posterior of the buccal mass. The fused band passes directly back to the origin near the midline of the diaphragm. The right tentacular retractor muscle passes between the male and female components of the reproductive system to its origin near the midline of the diaphragm. The left tentacular retractor muscle is split into a main branch that originates from the floor of the body cavity on the left side. The other branch is very slender, almost nerve-like. This branch extends backward toward an origin near the midline of the diaphragm thus preserving an overall pattern one might describe as converging. This pattern is disrupted only by the anomalous branch of the left tentacular retractor. We did not find a retensor muscle.

Digestive System: The jaw bears fine, evenly spaced incised lines but is not ribbed. The radula is of the usual arionid type, with the central row of teeth tricuspid, the inner lateral rows bicuspid and the outer rows tending toward elongation of the mesocones and reduction of the ectocones. The crop is large but otherwise unremarkable. The short, slender intestine makes three looping turns before arriving at the anal pore.

Holotype: From type locality, on cardboard cover-objects used to sample gastropods in a coniferous stand of mixed old-growth and naturally regenerated mature second-growth forest at elevation of 65–80 m; collected by J. Gray, L. Hyatt, C. Engelstoft, 7 Oct. 2002, Royal British Columbia Museum, RBCM 009-00035-001.

Paratypes: (1) Near summit of Mt. Genevieve, Graham Island (53°33.9′ N, 132°5.6′ W), from cardboard cover-objects in alpine meadow at elevation of about 800 m; collected by Luke Hyatt, 16 Oct. 2002, RBCM 009-00036-001; (2) mid-slope of Mt. Genevieve (Sleeping Beauty Trail; 53°15.8′ N, 132°12.9′ W), from cardboard cover-objects in old-growth coniferous forest at elevation of 340 m, collected by Kristiina Ovaska, Lennart Sopuck, and Berry Wijdeven, 22 Sep. 2004, Carnegie Museum of Natural History, CM97971 and RBCM 009-00038-001.

Type Locality: 13 km southeast of Port Clements, Graham Island (53°34.6′ N, 132°6.6′ W), Queen Charlotte Islands, British Columbia, Canada; a coniferous stand of mixed old-growth and naturally regenerated mature second-growth forest at elevation of 65–80 m.

Other Material Examined: Collected from Moresby Island by Kristiina Ovaska and Lennart Sopuck from under rocks or within krummholtz hummocks in subalpine meadows: (1) Yatza Mountain (52°21.5′ N, 131°26.0′ W), elevation 170–210 m, 14 Sep. 2003, RBCM 009-00037-001; (2) Mt. Oliver (52°42.9′ N, 132°1.4′ W), elevation 650 m, 14 Sep. 2004, RBCM 009-00039-001; (3) unnamed mountain near Kostan Inlet (52°34.7′ N, 131°44.0′ W), elevation 280 m, 14 Sep. 2004, RBCM 009-00041-001; (4) unnamed mountain near Sunday Inlet (52°37.9′ N, 131°50.4′ W), elevation 475 m, 14 Sep. 2004, RBCM 009-00040-001; (5) from within leaf litter along bank of small stream in old-growth coniferous forest: Louscoone Inlet (52°10.0′ N, 131°12.7′ W), elevation < 50 m, 17 Sep. 2004; RBCM 009-00042-001.

Etymology: The specific name (used as a name in apposition) *gwaii* means "island" or "home" in the Haida language and refers to the archipelago the slugs inhabit.

Natural History: The ten sites where the species was found ranged from lowland coniferous forest, dominated by Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*), to subalpine tundra. The species was seldom found in lowland forest (2 sites), although most extensive search effort was in this habitat. It was more frequently encountered at mid-elevation forest containing yellow cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), and/or shore pine (*Pinus contorta*), and in subalpine meadows and mountain slopes. The subalpine habitats were very moist with scattered, stunted (< 2 m tall) trees and bushes (*P. contorta*, *C. nootkatensis*, *T. mertensiana*, and *Juniperus* sp.) and swales of grasses, heather, and crowberry (*Empetrum nigrum*). In these habitats, we found slugs under rocks or within hummocks of ground vegetation. At the forested sites, we located the species by using cardboard cover-objects (see Methods); only one individual was found during visual searches of the forest floor. We found the smallest juveniles, about 2 mm in extended length, on 27–28 Jul. and 26 Sep. 2002 at a lowland site (Site 1 in Figure 1). We found larger juveniles and adult-sized individuals (> 10 mm in extended length) from September to November, 2002–2004. Longevity and life stages at which the slugs survive winter are unknown.

Possible Taxonomic Relationships: Of the previously described species, the new species most closely resembles small species of *Hemphillia* (*H. glandulosa*/*H. burringtoni* species complex). It differs from them externally by a mantle that completely covers the shell plate, which in the new species is calcareous, by dense, pointed papillae that cover the sides and the tail as well as the mantle, and by an unkeeled tail, and internally by an unusual configuration of buccal and tentacular retractors (Table 2).

DISCUSSION

The terrestrial gastropod fauna of Haida Gwaii is depauperate when compared to more southern areas along the Pacific coast, probably reflecting the isolation and harsh, northern climate of the archipelago; 18 native species were detected in contrast to over 35 species on Vancouver Island (Forsyth, 2004). With the notable exception of the new slug, *Staala gwaii*, all species of gastropods found during the surveys also occur on Vancouver Island and the coastal mainland of southern British Columbia. However, systematic relationships of some groups such as *Prophysaon*, *Pristiloma*, and *Vertigo* from western North America have not been examined recently, and genetic or detailed morphological studies could reveal differences among populations from Haida Gwaii and farther south. In particular, the unusual, clear-shelled *Pristiloma*, attributed herein to *P. stearnsii*, requires further investigation.

Curiously, we detected only infrequently two species that are relatively common on Vancouver Island and the lower mainland of British Columbia, *Nesovitrea binneyana* and *Euconulus fulvus*. Both snails were present in thermal meadows on Hotspring Island; *N. binneyana* also occupied sand dune habitat near Masset, Graham Island. We encountered *Cryptomastix germana* at only two sites within pockets of dense riparian herbaceous vegetation. This species has been reported previously from one Moresby Island locality (Forsyth, 2000). Some species (*Planogyra clappi*, *Cryptomastix germana*) probably exist at or near their northern limits of distribution in Haida Gwaii.

The new species of slug is of particular interest because it is possibly a relic of an ancient lineage that has survived several periods of glaciation on the archipelago. Ice-free refugia existed in various locations along the North Pacific coast from the Aleutian Islands to Vancouver Island during Pleistocene glaciations, and such refugia could have permitted the persistence of this and other endemic and disjunct species known from the islands through this and earlier glacial episodes. Paleoecological evidence exists for lowland ice-free refugia in Haida Gwaii at the height of the Wisconsin glacial epoch (Warner et al., 1982), but a continuous record of micro- or macro-fossils through this period is lacking. Some mountain tops in the Queen Charlotte Range are also thought to have remained as ice-free nunataks throughout glacial periods (Heusser, 1989) and probably supported organisms such as bryophytes (Schofield, 1989a) that are able to exist in small microhabitats and withstand harsh conditions. The slug could conceivably also have persisted in nunataks, as it is presently found in isolated mountain top habitats.

Some endemics on the archipelago appear to be of relatively recent origin as a result of rapid morphological evolution in post-glacial times within the past 15,000–16,000 years (e.g., carabid beetles of the genus *Nebria*: Clarke et al., 2001; Haida Gwaii black bear, *Ursus americanus carlottae*: Byun et al., 1997), whereas others are thought to be much older. Ancient, possibly Tertiary origins have been postulated for relic species of bryophytes that show unusual, disjunct distribution patterns (Schofield, 1989a).

Preliminary molecular analyses suggest that the lineage containing *Staala gwaii* is old and has split from *Hemphillia*, the presumed sister taxon, several million years ago (Wilke, 2004; Thomas Wilke, Animal Ecology & Systematics, Justus Liebig University Giessen, Giessen, Germany, pers. comm.), lending support to the notion that the slugs survived several glacial periods in refugia on the islands or elsewhere along the northwest coast of North America. Several species of plants endemic to the northwest coast have scattered and disjunct distributions (Calder and Taylor, 1968; Taylor, 1989; Ogilvie, 1989). Examples of endemic plants that co-occur with the slug in subalpine habitats in Haida Gwaii include *Geum schofieldii*, *Ligusticum calderi*, *Saxifraxa taylori*, and *Senecio moresbiensis* on Mt. De la Touche; *Ligusticum calderi* and *Saxifraga taylori* on Mt. Yatza; *Ligusticum calderi* on Mt. Oliver; *Saxifraga taylori* and *Senecio moresbiensis* on an unnamed mountain east of Blue Heron Bay (plant distribution from unpublished data files by Parks Canada).

Further surveys along the northwest coast of mainland British Columbia are needed to document the extent of the distribution of *Staala gwaii* and to explore the existence of other undiscovered species and populations. Comparative studies with other western North American and northeast Asian forms are also desirable, as they have potential to shed light on the evolution and biogeography of western North American slugs.

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