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Crepidula adunca and Crepidula norrisiarum have  
overlapping shell size and broadly concordant  
distributions**

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# The Biological Bulletin

## Size doesn't matter: integrative taxonomy shows *Crepidula adunca* and *Crepidula norrisiarum* have overlapping shell size and broadly concordant distributions.

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<b>Abstract:</b>	<p>The calyptraeids <i>Crepidula adunca</i> and <i>Crepidula norrisiarum</i>, both direct-developers, are abundant in the shallow waters of the northeastern Pacific. They have long been considered as two allopatric species that live on different hosts and differ in body size. In this study, we rigorously test this historical hypothesis by assessing molecular taxonomy, museum records, new morphological and host observations, and population genetic structure along the northeast Pacific coast. Results show that contrary to previous understanding, the distributions of the two species largely overlap, and that size does not effectively distinguish them, especially in the northern part of the range where the nominal "<i>C. adunca</i>" has been studied. Newly recognized northern occurrences of <i>C. norrisiarum</i> demonstrate that both species have similar, disrupted distributions that range from British Columbia through Southern California. Neither species is reported to occur on the outer shores of Southern Washington or Oregon, the exception being records of <i>C. adunca</i> at Cape Arago, Oregon. Despite this apparent geographic gap, neither species shows appreciable genetic differentiation between the northern and southern parts of their ranges. Despite that body size has been used to distinguish these species, our observations do not support body size as a species-specific trait; rather, they support a new hypothesis that body size variation</p>



reflects regional differences in host use and host availability.

1 **Running head:** Biogeography and hosts of *Crepidula*

2 **Manuscript title:** Size doesn't matter: integrative taxonomy shows *Crepidula adunca* and  
3 *Crepidula norrisiarum* have overlapping shell size and broadly concordant distributions.

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18

19 **Abbreviations:**

20 ABGD: Automatic Barcode Gap Discovery

21 CAS: California Academy of Sciences: San Francisco

22 CASIZ: Unique voucher identifier of Invertebrate Zoology collections at the California Academy  
23 of Sciences: San Francisco

24 CMN: Canadian Museum of Nature: Ottawa

- 25 *coxI*: Cytochrome c oxidase I
- 26 DFO: Fisheries and Oceans Canada: Canada
- 27 FMNH: Field Museum of Natural History: Chicago
- 28 LACM: Natural History Museum of Los Angeles County: Los Angeles
- 29 NHMUK: Unique voucher identifier at Natural History Museum: London
- 30 RBCM: Royal BC Museum: Victoria
- 31 USNM: National Museum of Natural History: Smithsonian Institution: Washington: D.C.
- 32 AK: Alaska
- 33 BC: British Columbia
- 34 WA: Washington
- 35 OR: Oregon
- 36 CA: California
- 37
- 38 **Keywords:** slipper limpets; northeastern Pacific; *coxI*; systematics; phylogeography; mutualism.
- 39
- 40

41 **Abstract**

42 The calyptraeids *Crepidula adunca* and *Crepidula norrisiarum*, both direct-developers, are  
43 abundant in the shallow waters of the northeastern Pacific. They have long been considered as  
44 two allopatric-species that live on different hosts and differ in body size. In this study, we  
45 rigorously test this historical hypothesis by assessing molecular taxonomy, museum records, new  
46 morphological and host observations, and population genetic structure along the northeast Pacific  
47 coast. Results show that contrary to previous understanding, the distributions of the two species  
48 largely overlap, and that size does not effectively distinguish them, especially in the northern part  
49 of the range where the nominal “*C. adunca*” has been studied. Newly recognized northern  
50 occurrences of *C. norrisiarum* demonstrate that both species have similar, disrupted distributions  
51 that range from British Columbia through Southern California. Neither species is reported to  
52 occur on the outer shores of Southern Washington or Oregon, the exception being records of *C.*  
53 *adunca* at Cape Arago, Oregon. Despite this apparent geographic gap, neither species shows  
54 appreciable genetic differentiation between the northern and southern parts of their ranges.  
55 Despite that body size has been used to distinguish these species, our observations do not support  
56 body size as a species-specific trait; rather, they support a new hypothesis that body size variation  
57 reflects regional differences in host use and host availability.

58

59

60 **Introduction**

61 Species that form mutualistic relationships are subject to selective pressures imposed by their host  
62 and environment, and this can have an important impact on their phenotypic traits, behavior, and  
63 geographic range (Boucher, 1982; Afkhami *et al.*, 2014, Pechenik *et al.*, 2020). Well-studied  
64 examples of eco-evolutionary changes induced by mutualism are found in terrestrial and marine  
65 systems, from viruses to large mammals, including flowering plants and their animal pollinators or  
66 seed dispersers (Fleming and Estrada, 1993; Moeller *et al.*, 2012). Marine examples have also been  
67 explored and include fish-cleaning shrimps that develop specific behavioral and morphological  
68 traits to attract their fish customers (Vaughan *et al.*, 2017; Horka *et al.*, 2018), and partner fidelity  
69 between sponges, corals and their symbiotic bacteria and zooxanthellae (Muller-Parker *et al.*,  
70 2015). Mutualism can involve close associations or more diffuse ones that allow switches to novel  
71 partners, or even to abandonment of mutualism (Toby Kiers *et al.*, 2010; Freeman *et al.*, 2015;  
72 Fang *et al.*, 2017). Such processes can impact the geographic range of each mutualistic partner. In  
73 some cases, habitat fragmentation, population structure, and mode of dispersal may also impact  
74 whether the form of mutualism is close *versus* diffuse and affect the spatial dynamics of the  
75 interaction (Amarasekare, 2004).

76  
77 The sedentary, suspension-feeding gastropod mollusks known as slipper limpets  
78 (Calyptraeidae: Crepidula) provide a useful system for studying the impact of mutualism on  
79 phenotypic traits, behavior, and species distribution patterns. Numerous species in this group  
80 form long-term epibiotic associations with other invertebrates but many can also be  
81 opportunistically found on rocks and other hard substrates (Vermeij, 2020). Because the slipper  
82 limpet lacks an operculum and has a large aperture, the edges of the shell must grow to closely fit  
83 the curvature and irregularities of the substrate in order to protect the internal body.

84 Consequently, shell shapes and body size of calyptraeids often vary within species and among  
85 regions, being flat, arched, concave, scalloped, or twisted, depending on substrate shape and host  
86 identity (Coe, 1942; Vermeij *et al.*, 1987; Von Tungeln and Pernet, 2017). The phenotypic  
87 plasticity of slipper limpets has led to considerable taxonomic confusion and consequent  
88 misleading or ambiguous results of ecological studies, when the taxonomy is poorly resolved.  
89 Here we apply an integrative taxonomic approach to resolve one such taxonomic problem.

90  
91 For over 100 years, *Crepidula adunca* and *Crepidula norrisiarum*, both abundant shallow  
92 water calyptraeids of the northeastern Pacific, have been thought to have mostly allopatric  
93 distributions, to live on different hosts, and to have different shell morphologies and body sizes.  
94 *Crepidula adunca* is known for being a small, dark brown species found mostly intertidally on  
95 the gastropod *Tegula funebris* in central California, or intertidally on *Calliostoma ligatum* as  
96 well as on *T. funebris* in Washington State and British Columbia. *Crepidula norrisiarum* is  
97 known for being a large subtidal species, light rust-brown in color with brown radiating lines, that  
98 lives primarily on the large gastropod *Norrisia norrisii* in Southern California. Recently, a large-  
99 scale assessment of biodiversity and community dynamics of littoral gastropods in British  
100 Columbia, Canada, showed two species with similar body size and shell morphologies co-occur  
101 there (Castelin *et al.*, 2016). Individuals from the same sites could not be differentiated by shell  
102 morphology and had mitochondrial DNA and a nuclear marker divergence levels similar to those  
103 observed between other congeneric gastropods (Castelin *et al.* 2016). These observations  
104 challenged the species concepts and the historical hypothesis of two allopatric species varying in  
105 size and morphology, and raised questions regarding host-specificity, as the large, Californian  
106 host of *C. norrisiarum*, *N. norrisii*, is not present as far north as British Columbia. These  
107 observations led to an alternative hypothesis that shell morphology and body size are misleading

108 with respect to species identity and instead reflect regional differences in host use and host  
109 availability.

110 The present study investigates the geographic distributions and population genetic  
111 structure of *C. adunca* and *C. norissiarum* along the Northeast Pacific coast, and documents new  
112 morphological diagnostic traits to distinguish them. We also report host records based on  
113 available museum records and field observations to enable future investigation on the spatial  
114 dynamics of mutualism in these species. Our aim was to redress the relative lack of available data  
115 from the north (British Columbia), but we also conducted new collecting in the south  
116 (Washington to California) to add to existing samples. Finally, by re-describing the two species,  
117 we provide key diagnostic characters to distinguish them and give a more precise description of  
118 their respective distribution, habitats, and host preferences. The present study enables and  
119 encourages marine ecologists to: (i) accurately distinguish between *C. adunca* and *C.*  
120 *norrisiarum*; (ii) consider their co-occurrence when planning sampling strategies along the  
121 northeast Pacific coast; (iii) carefully document host use; (iv) pay extra attention to potential  
122 taxonomic misidentifications in the scientific literature.

123

## 124 **Materials and Methods**

125

### 126 ***Study area and specimen collection***

127 Slipper limpets *C. adunca* and *C. norrisiarum* were collected between 2012 and 2019 (Table 1).  
128 Samples collected along the coast of British Columbia (BC) were obtained by hand either during  
129 dive surveys to 10 m depth or shore-based expeditions directed by Fisheries and Ocean Canada  
130 (DFO) and the Royal British Columbia Museum (RBCM), Victoria, BC, Canada. Samples from  
131 Washington (WA) were collected by hand at low tide from the intertidal zone by Collin (2000a;

132 2000b; 2004) (Fig. 1A). Animals were sampled in California (CA) in the intertidal by Eernisse,  
133 by dive surveys by personnel of the Channel Islands National Park (Fig. 1B), and material  
134 collected for past projects was also used (Collin (2000a; 2000b; 2004). In addition to the 35  
135 specimens of *C. adunca* and *C. norrisiarum* available from Castelin *et al.* (2016), 12 individuals  
136 from BC (Ucluelet and Tofino) and 19 individuals from CA (San Simeon, Yellow Bank, and  
137 Santa Barbara) were newly-collected in this study for DNA sequencing. Two additional  
138 specimens, one from WA and one from CA with previously published sequences (Collin, 2003a),  
139 were added to the final dataset (Table 1).

140         After collection, all specimens were preserved for molecular analysis. Soft tissues were  
141 preserved in 95% ethanol, while shells were dried and kept intact for further study. Vouchers  
142 from Canadian samples were deposited in the biological collections of the RBCM, and those  
143 from the CA samples were deposited in the Natural History Museum of Los Angeles County  
144 (LACM) (Table 1).

145

#### 146 ***PCR amplification and DNA sequencing***

147 Total genomic DNA was extracted using the NucleoSpinR 96 Tissue kit (Macherey-Nagel,  
148 Allentown, PA, United States) following manufacturer's instructions. A fragment of the  
149 mitochondrial *cox1* was amplified using universal primers LCOI1490 and HCO2198 (Folmer *et*  
150 *al.*, 1994) using conditions described in Castelin *et al.* (2016). PCR products were purified with  
151 ExoSAP-IT (Affymetrix, Santa Clara, CA, United States) prior to bidirectional sequencing using  
152 PCR primers and BigDye Terminator v3.1 chemistry. Cycle sequencing reactions were purified  
153 using ethanol/EDTA precipitation followed by an additional ethanol wash and were  
154 electrophoresed using an ABI 3730xL DNA Analyzer (Applied Biosystems, Waltham, MA,



155 United States). Double stranded sequences were assembled and edited using CodonCode Aligner  
156 v. 4.1.1 (CodonCode Corporation, Dedham, MA, United States).

157

158 ***DNA sequence alignment and molecular analysis***

159 Alignments were generated using MAFFT v. 7 (Katoh *et al.*, 2002; Katoh and Toh, 2010).

160 Sequences were aligned using the FFT-NS-I option, which is recommended for alignments of  
161 closely-related sequences with global homology (Katoh and Toh, 2008). The offset value was set  
162 at 0.1, as gaps were not expected. The accuracy of automatic alignments was confirmed by eye  
163 and protein coding sequences were translated into amino acids using MEGA v. 5.05 (Tamura *et*  
164 *al.*, 2011) to check for gaps and stop codons. Newly produced sequences from Canada were  
165 deposited in BOLD Systems in the project DS-CREPID West Coast *Crepidula* (SGPBS001-20 to  
166 SGPBS011-20) and in GenBank (MN992952 - MN992958, MN992960 - MN992961). Those  
167 from CA were deposited directly in GenBank (OK526437 - OK526467) (Table 1).

168 The Automatic Barcode Gap Discovery (ABGD) method of Puillandre *et al.* (2012) was  
169 applied to our *cox1* dataset to assign newly-sampled specimens to species (i.e., to *C. adunca* or *C.*  
170 *norrisiarum*) using sequences from existing phylogenies (Collin, 2003a; Castelin *et al.*, 2016).  
171 The ABGD method was implemented using the online version of the program with the relative  
172 gap width (X) set to 10.

173 Within each species, identical sequences were identified using DnaSP version 6 (Librado  
174 and Rozas, 2009). To visualize the genealogical relationships among haplotypes and geography,  
175 median-joining networks (MJN) were constructed for both species using the program  
176 NETWORK 10.2 (Bandelt *et al.*, 1999) with equal weights for variable sites (epsilon = 0) using

177 the connection cost calculation method. To delete superfluous median vectors and links that are  
178 not contained in the shortest tree, we ran a postprocessing maximum parsimony calculation.

179 Genetic differentiation within each species was assessed using Arlequin 3.5.2.2 with an  
180 analysis of molecular variance (AMOVA; Excoffier *et al.*, 1992). Individuals within each species  
181 were partitioned into northern (BC, WA) and southern (CA) localities. Estimates of  $\Phi_{ST}$  were  
182 conducted using a distance matrix with 10,000 permutations and the pairwise difference model.  
183 Significance of  $\Phi$ -statistics was calculated from 10,000 replicate analyses based on samples  
184 drawn randomly and an alpha value of 0.05 (Excoffier and Lischer, 2010). In addition, within-  
185 species, genetic diversity between northern and southern populations was assessed using number  
186 of segregating sites ( $S$ ), nucleotide diversity ( $\pi$ , mean number of pairwise differences), and  
187 haplotype diversity ( $H_d$ ).

188

### 189 ***Morphological observations***

190 Shell morphology of individuals in each genetic group (as identified by the ABGD method) was  
191 examined and overall shape and size of each individual were recorded as was their color, shell  
192 apex morphology, and extent of excavation of the apex below the shelf. Maximum shell length  
193 was measured using a precision caliper. The following features of the soft anatomy: osphradium  
194 morphology, penis morphology, and the shape of the female genital papilla were examined for a  
195 subset of individuals as these features have previously been shown to vary among closely related  
196 calyptraeid species (Collin, 2000a; 2003b; 2019). The soft anatomy was examined for animals  
197 from both species, collected from south central CA and from *C. norrisiarum* from San Juan  
198 Island, WA. The shells of the type material of *C. adunca*, *C. norrisiarum*, and all species  
199 commonly synonymized with either species were examined either in person or using digital  
200 images requested from curators. If the type could not be found, we examined the illustrations in

201 the original description. Shell morphology was examined for more than 100 specimen lots from  
202 the Los Angeles County Museum, Invertebrate Zoology collections of the California Academy of  
203 Sciences (CASIZ), RBCM and Canadian Museum of Nature (CMN), including the syntypes of *C.*  
204 *norrisiarium* (LACM 1027).

205

### 206 ***Host observations***

207 Records, including our own, were reviewed to determine what host species were used by the two  
208 *Crepidula* species. These included museum records and *in situ* images of *C. adunca* and *C.*  
209 *norrisiarum* posted on iNaturalist (2021) when diagnostic features including apex position,  
210 posterior slope shape (hooked or blunt), and/or shell color were clearly-identifiable.

211

## 212 **Results**

### 213 ***Molecular results***

214 A total of 68 *cox1* sequences of 657 bp length were analyzed, of which 31 were newly-produced  
215 in this study (Table 1) and 37 were obtained from previous studies (Collin, 2003a, b; Castelin *et*  
216 *al.*, 2016). We found no evidence of *cox1* pseudo-gene amplification; no sites were scored as  
217 ambiguities by the software and no translations contained any stop codons. The ABGD method  
218 estimated 10 *a priori* thresholds, 9 of which led to partitions that split individuals into two groups  
219 separated by 11% divergence and associated with morphological differences (see taxonomic  
220 section). A total of 48 individuals were attributed to a mtDNA clade corresponding to *C. adunca*  
221 and 20 individuals to the reciprocally monophyletic group for *C. norrisiarum*.

222 The 48 individuals of *C. adunca* comprised 9 haplotypes, with 40 individuals sharing 4  
223 haplotypes in the north (BC = 36 individuals, 4 haplotypes; WA = 4 individuals, 1 haplotype), and  
224 8 individuals sharing 5 haplotypes in the south (CA). Consequently, although more individuals

225 were collected in the north, haplotype and nucleotide diversity was lower in the north ( $Hd = 0.146$ ,  
226  $\pi = 0.2$ ) than in the south ( $Hd = 0.857$ ,  $\pi = 2.07$ ) (Table 2). No haplotypes were shared between the  
227 north and south.

228 The 20 individuals of *C. norrisiarum* displayed 13 haplotypes, with 12 individuals sharing  
229 7 haplotypes in the north (BC = 11 individuals, 7 haplotypes; WA = 1 individuals, 1 haplotype),  
230 and 8 individuals sharing 6 haplotypes in the south (CA). Contrary to *C. adunca*, haplotype and  
231 nucleotide diversity was high both in the north ( $Hd = 0.833$ ,  $\pi = 1.68$ ) and south ( $Hd = 0.892$ ,  $\pi =$   
232  $2.14$ ). No haplotypes were shared between the north and south.

233 In both species, haplotype networks showed geographic structure between northern and  
234 southern regions (Fig. 2-3). In *C. adunca*, a major northern haplotype was shared among  
235 individuals from the west coast of Vancouver Island, BC (Brooks Bay, Ucluelet, Port Renfrew)  
236 and individuals from the Pacific coast of the Olympic Peninsula, WA (Cape Alava). This major  
237 haplotype was separated by one to two mutations from four single haplotypes from Brooks Bay  
238 and Ucluelet (BC) and from one haplotype from San Simeon (CA), itself separated by one to four  
239 mutations from three haplotypes from the same area (CA) (Fig.2). In *C. norrisiarum*, three  
240 groups could be distinguished: a main central group including five haplotypes shared among  
241 individuals from Yellow Bank and Santa Barbara (CA), Tofino-Ucluelet and Brooks Bay (BC),  
242 from which derived a second group including only individuals from Vancouver Island (BC), and  
243 a third including only genetically distant individuals from Yellow Bank (CA) (Fig. 3).

244 Within each species, significant levels of genetic heterogeneity were detected between  
245 northern and the southern localities. In *C. adunca*, genetic heterogeneity between northern and  
246 southern regions ( $\Phi_{ST} = 0.686$ ,  $P < 10^{-5}$ ) accounted for 69% of the total variance and variation  
247 within regions accounted for 31% ( $P < 10^{-5}$ ). In *C. norrisiarum*, genetic heterogeneity between

248 northern and southern regions ( $\Phi_{ST} = 0.369$ ,  $P < 10^{-5}$ ) accounted for 37% of the total variance,  
249 and variation within regions accounted for 63% ( $P < 10^{-5}$ ).

### 250 ***Morphology***

251 Detailed examination of our samples and type material shows that *C. adunca* and *C. norrisiarum*  
252 can be distinguished based on internal shell characters, and that these diagnostic features are  
253 present in the holotype of *C. adunca* and four syntypes of *C. norrisiarum*. *Crepidula adunca* (Fig.  
254 4) is characterized by an elevated, hooked, shell apex, which often creates a strongly concave  
255 vertical posterior shell outline, and a clear excavation or dimple in posterior portion of the shelf  
256 when the cleaned shell is viewed from the aperture. This is consistent from small juveniles  
257 (<3mm) to adult specimens. *Crepidula norrisiarum* (Fig. 5) is characterized by a more appressed  
258 and somewhat blunt and more rounded apex which may be either at the level of the aperture or  
259 somewhat above the aperture. When elevated, the apex is less high and less distinct than that  
260 observed in *C. adunca*, and has a relatively straight vertical posterior shell outline. *Crepidula*  
261 *norrisiarum* also lacks the excavation or dimple in the shelf and the shell exterior often has a  
262 pinkish tint and a somewhat checkered pattern (Fig. 5). Nearly all shells have either one or the  
263 other of these suites of characters, although some samples are intermediate in morphology,  
264 making it difficult to distinguish some living individuals with certainty. The presence or absence  
265 of the dimple on the shelf, which can only be observed on dead shells, appears to be the most  
266 reliable feature to distinguish them.

267 The two species show distinct inter- and intra-specific variation in body size. *Crepidula*  
268 *adunca* reach sizes up to 27mm (depending on the host used) and the largest sizes seem to be  
269 attained subtidally. In contrast *C. norrisiarum* shows size dimorphism. In the San Juan Islands,  
270 WA, where this species is common on *Calliostoma ligatum*, *C. norrisiarum* usually does not

271 exceed 15mm (Collin, 2000b, 2003b; 2019), while it often reaches 30 to 40mm in the southern  
272 CA part of the range where it lives on *N. norrisii* (Collin, 2003c).

273         With respect to the soft parts, there are very slight differences in overall body color (Fig.  
274 6) and in the morphology of the osphradia. The head, body, mantle, and foot of *C. adunca* is  
275 bright white with fine opaque white speckles, while the body of *C. norrisiarum* is a cream color.  
276 The difference is not obvious unless the animals are observed side-by-side. Both usually have  
277 some black pigment on the mantle and dorsal area of the food pouch and head, but this is usually  
278 more pronounced in *C. adunca*. In *C. norrisiarum* from both northern and southern localities the  
279 osphradial leaflets are unevenly spaced (which is unusual in *Crepidula* species), with a central  
280 leaflet flanked on each side by a gap and lateral to that a small cluster of leaflets with a total of no  
281 more than 19 (see Fig. 6A and Fig. 7B in Collin, 2003b). The gap is very pronounced in large  
282 animals and less obvious or absent in smaller ones. The osphradium in *C. adunca* shows a similar  
283 arrangement with one central leaflet flanked by a gap on each side and then a cluster of leaflets,  
284 but the leaflets are relatively longer and the gap seems relatively shorter than in *C. norrisiarum*.  
285 In both species the number of leaflets increases in a similar way with shell length (data not  
286 shown). Other features of the soft anatomy that have been used to distinguish closely related  
287 species of *Crepidula*, like mode of development and gross morphology of the female genital  
288 papilla, did not show obvious differences between these two species.

289

### 290 ***Hosts***

291 *Crepidula adunca* and *C. norrisiarum* have been observed on various hosts, including a number  
292 of occasional hosts (Table 3, Fig. 7). Of the many host species, only *Tegula pulligo*, *Tegula*  
293 *brunnea*, *Calliostoma ligatum*, and *Alia carinata* have so far been associated with both *C. adunca*  
294 and *C. norrisiarum* (Table 3).

295 In the northern part of the range and in central CA, specimens of *C. adunca* were  
296 collected intertidally on their typical host, *Tegula funebris*. Interestingly, it has not been  
297 reported from *T. funebris* in southern CA, even though this species is relatively common there  
298 in the intertidal, nor does *C. adunca* seem to occur on the similar intertidal species, *T. gallina*,  
299 which replaces *T. funebris* to the south. In California *C. adunca* is known from the subtidal on  
300 *Tegula* spp. around Santa Barbara and on *Mitra idae* (Figure 7; R. Collin pers. obs.). In the  
301 northern part of the range, *C. adunca* was also commonly collected on *Lirabuccinum dirum* and  
302 occasionally on a number of other species. In BC, *C. adunca* has also been observed on snail  
303 shells occupied by hermit crabs as well as empty shells, as it has been in Oregon (R. Emlet, pers.  
304 com. 2019). *Crepidula adunca* was also sometimes found on rock in WA (RBCM 21-53-1) and  
305 the west coast of Vancouver Island (LACM 26030).

306 Southern CA specimens of *C. norissiarum* typically occurs subtidally attached to *Norrisia*  
307 *norrisii*, but we also observed some *C. norissiarum* on low intertidal specimens of *Tegula*  
308 *brunnea* and subtidal specimens of *T. pulligo* in central CA as far north as Monterey Co. In  
309 central CA, *C. norissiarum* was never observed on *Calliostoma ligatum*, while in WA and BC, it  
310 was most commonly collected attached to *Calliostoma ligatum* and occasionally *Tegula pulligo*.

311

## 312 ***Taxonomic Section***

### 313 ***Crepidula* Lamarck, 1799**

314 *Crepidula* Lamarck, 1799: 78. Type species: *Patella fornicata* Linnaeus, 1758.

315 *Ianacus* Mörch, 1852: 146. Type species: *Crepidula unguiformis* Lamarck, 1767.

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317 *Crepidula adunca* G. B. Sowerby I, 1825

318 *Crepidula adunca* Sowerby I, 1825 (App.): 7. Holotype NHMUK 1997150. No locality. (Fig. 4).

319 *Crepidula solida* Hinds, 1844: 53, pl. 16, figs 7–8. Type lost, Bodegas, California. 10 fathoms.

320 *Crepidula rostriformis* Gould, 1846: 160, 1856, pl. 32, fig. 482. Holotype USNM 5872. Strait of  
321 Juan de Fuca, Washington.

322 *Crepidula adunca* Sowerby I, 1825 Hoagland 1977 (in part)

323  
324 **Material sequenced.** KX069514 - KX069521; KX069523; KX069525 - KX069529; KX070349;

325 KX070351; MN992952 - MN992961; MT048416; OK526437 - OK526457 (Table 1). Other  
326 material examined includes the entire dry collection at LACM and at CAS as well as material in  
327 RC's personal collection collected from Diablo Canyon, California by Sean Andersen.

328

329 **Description**

330 **The shell** is typically smooth, uniform chestnut to dark brown (Fig. 4). The shell can appear  
331 ribbed when attached to a ribbed snail host, and the shape can take on the contours of the host.

332 **The shell** is typically oval but occasionally it is round when substrate is not limiting. **The shell**  
333 **length** of animals living on other snails can reach 27 mm, and one particularly unusual individual  
334 collected from a rocky substrate is 32.7 mm (LACM 26030). **The apex** is raised, usually nearly  
335 as high or higher than the body of the shell, and sharply hooked or beaklike. The apex is rostrate,  
336 often projecting beyond the posterior margin of the base (Fig. 4, Fig. 7A-C, Fig. 7E). **The shell**  
337 **interior** is dark chocolate brown with a white shelf or septum. **The septum** is flat, extends  
338 straight across, without a medial ridge, and extends anteriorly on both sides. There is a deep  
339 cavity like a dimple extending into the spire where the septum meets the posterior margin of the  
340 shell (Fig. 4). This cavity was clear in both juvenile (<3 mm) and adult shells, and is not observed



341 in *C. norrisiarum*. There are muscle scars adjacent to the anterior extensions of the septum on  
342 each side.

343

344 **External Anatomy** is overall similar to other *Crepidula* species. Observations reported here are  
345 for *C. adunca* from Diablo Canyon, CA. The body is white with small opaque white speckles on  
346 the mantle and the top of the neck. There is black pigment on the top of the tentacles, snout and  
347 lips, as well as on the osphradium and the tip of the gills. These markings are similar but more  
348 pronounced than in *C. norrisiarum*. The lips are almost symmetrical making this species easy to  
349 distinguish from *C. naticarum*, a species only reported to live on naticid gastropod shells  
350 occupied by hermit crabs, in which the lips, head and neck are asymmetrical. The foot is  
351 extensible but retains the oblong, blunt shape when extended and does not form propodial  
352 tentacles and there are no mesopodial flaps. The osphradium is monopectinate, the leaflets are  
353 somewhat unevenly spaced in all but small males. One central leaflet is flanked on each side by a  
354 gap, followed by a cluster of leaflets. Leaflets are longer in *C. adunca* than in *C. norrisiarum* and  
355 the gap is less pronounced in *C. adunca*. The food pouch is right of the midline (when viewed  
356 from the aperture) and the rim does not form a large flap as it does in some *Crepidula* species.

357

358 **Development** is direct from large eggs. Hatching length has been previously reported as 1.19mm  
359 from naturally hatching broods of 6 females from Central CA (Putnam, 1964) which can be  
360 clearly identified as *C. adunca* from the illustrations in the paper. Coe (1949) reported eggs size  
361 as 400-420  $\mu\text{m}$  from southern CA but the identity of his material is less clear. Uncleaved eggs  
362 from 2 clutches of animals collected in Diablo Canyon had mean hatching sizes of 503 $\mu\text{m}$  and  
363 486 $\mu\text{m}$ . The embryos from these animals have a large head vesicle which is not filled with yolk,  
364 the velum is a simple rudiment at the base of the tentacles. Only late stage embryos were

365 observed but they appear to have only a single large larval “kidney cell”, as compared to *C.*  
366 *norrissiarum*, which has a cluster of cells. Mean hatching size per clutch from Diablo Canyon  
367 ranged from 1044µm to 1426µm for 8 clutches.

368  
369 **Notes:** Animals collected from San Juan Island, WA and referred to as *C. adunca* in Collin  
370 (2000; 2003a,b; 2004) are actually *C. norrissiarum*. This is also likely the case for Herstoff and  
371 Iyengar (2011) who collected animals at the same site and partially for Vermeij *et al.*, (1987) who  
372 included material from both species, *C. norrissiarum* from San Juan Island, WA (Fig. 1 in  
373 Vermeij *et al.*, 1987) and *C. adunca* from Tatoosh Island, WA.

374 Examination of the types of *C. rostriformis* and the figures in the description of *C. solida*  
375 clearly show the rostrate apex and cavity or dimple in the shelf extending into the shell apex (Fig.  
376 4), which supports the conclusion that they are junior synonyms of *C. adunca*. Hoagland (1977)  
377 lists *C. uncata* Menke 1847 from Panama as a synonym, but this is almost certainly one of the  
378 related southern species, like *C. incurva*, that also live on gastropod shells. The Miocene fossil  
379 *Crypta rostralis* Conrad 1865 from the Astoria formation in Oregon could be either *C. adunca* or  
380 *C. norrissiarum* (or an earlier distinct species) based on our examination of the dorsal view of the  
381 holotype (USNM 110447) published in Moore (1963). We were not able to examine this shell as  
382 it could not be located in the USNM collections.

383  
384 **Distribution:** Museum samples with diagnostic shell features indicate that the range extends at  
385 least from Cohen Island, Kachemak Bay, AK (LACM 59-23.18) to Santo Thomas, northern Baja  
386 California, Mexico (LACM 161700). This species is rare in the intertidal in southern California,  
387 especially south of Santa Barbara Co. It is also rare between northern California and northern  
388 Washington state, where it has been reported only from Cape Arago, OR (e.g., LACM collections

389 AHF 1989-42 through AHF1491-42; AHF 1492-42 . In the Strait of Juan de Fuca, *C. adunca* was  
390 found only on the outer shores, west of Victoria, BC and west of Tongue Pt., WA.

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393 ***Crepidula norrisiarum* Williamson, 1905**

394 *Crepidula rugosa norrisiarum* Williamson, 1905: 50. Syntypes LACM 1027. San Pedro Bay,  
395 California.

396 *Crepidula norrisiarum* Williamson, 1905. Hoagland 1977 (In part)

397 *Crepidula adunca* Sowerby 1825. Hoagland 1977 (In part)

398 *Crepidula norrisiarum* Williamson, 1905. McLean (In part)

399 *Crepidula norrisiarum* Williamson, 1905. Collin 2003a, b

400 *Crepidula adunca* Sowerby 1825 Collin 2000; 2003a,b

401 *Crepidula norrisiarum* Williamson, 1905. Collin 2019

402

403 **Material sequenced.** AF546047; AF550487; KX069531; KX069533; KX069535; KX069537;

404 KX070358; OK526458 - OK526467 (Table 1). Other material examined includes entire

405 collection at LACM and CAS and animals included in Collin 2003a,b represented by vouchers:

406 FMNH282185, FMNH282173 - FMNH282175 from Naples Reef, Santa Barbara county, CA and

407 animals included in Collin (2000a,b).

408

409 **Diagnosis:**

410 **The shell** exterior is typically smooth, light rust-brown with brown radiating lines or checkers

411 and often with a pinkish apex (Fig. 5). The radiating lines are not evident in many northern

412 specimens of *C. norrisiarum*. The thin periostracum is sometimes worn away. The shell can

413 appear ribbed when attached and growing on a ribbed snail host and the shape can take on the  
414 contours of the host. **The shell** is typically oval but occasionally it is round when substrate is not  
415 limiting. **The shell length** reaches 40 mm in the southern range where it is found on the larger  
416 snail host, *N. norrisii*. In the northern range the shell length is typically to 15 mm. **The apex** is  
417 soft-pointed to blunt, projecting less than in *C. adunca*, and often almost symmetrical, near the  
418 midline, with a slight curve or tilt to the right (Fig. 5; Fig. 7F, G). The apex extends slightly past  
419 the posterior margin, usually overhanging it. The apex is generally on the lower half of the shell,  
420 sometimes at the level of the aperture, and is seldom the highest part of the shell. **The interior** is  
421 pink to tan, with a white septum. **The septum** is broadly U-shaped, and the sides extend forward.  
422 There are two muscle scars, each adjacent to the anterior extensions of the septum. The septum  
423 does not have a cavity where the septum meets the posterior shell margin (Fig. 5). The lack of a  
424 cavity under the spire (apex) was remarked upon by Williamson, 1905 in his original description  
425 of *C. norrisiarum*. In the northern population, the shell is more arched, the apex moderately  
426 raised, typically higher than in the southern form, and projecting beyond the posterior margin  
427 (Fig. 7G). This is likely due to the animals growing to fit smaller hosts.

428  
429 **External Anatomy** is overall similar to other *Crepidula* species. Observations reported here are  
430 from *C. norrisiarum* from San Juan Island, WA and from Santa Barbara, CA. The body is cream-  
431 colored (Fig. 5A) with sparse small opaque white speckles on the mantle and the top of the neck.  
432 There is a dusting of black pigment on the top of the tentacles, snout and lips, as well as on the  
433 osphradium and sometimes on the tip of the gills. The lips are almost symmetrical making this  
434 species easy to distinguish from *C. naticarum*, in which the lips, head and neck are asymmetrical.  
435 The foot is extensible but retains the oblong, blunt shape when extended and does not form  
436 propodeal tentacles and there are no mesopodial flaps. The osphradium is monopectinate, the

437 leaflets are unevenly spaced in all but small males (see Fig. 7A in Collin 2003b). One central  
438 leaflet is flanked on each side by a gap, followed by a cluster of leaflets. Leaflets are shorter than  
439 in *C. adunca*. The food pouch is right of the midline (when viewed from the aperture) and the rim  
440 does not form a large flap as it does in some *Crepidula* species. The penis is evenly tapered and  
441 slightly flattened with a groove extending to the end. The female genital papilla extends free into  
442 the mantle cavity, it is not grooved.

443  
444 **Development** is direct from large eggs. In the San Juan Islands, uncleaved egg size was reported  
445 as 260-320µm (Collin 2000) and 240µm (Strathmann, 1987), and hatching size was 1.5-2.7 mm  
446 (Collin 2000) or 1.0-2.0 mm (Strathmann, 1987). In southern California uncleaved egg size from  
447 the single brood from a definitive *C. norrisiarum* collected from a *N. norrisii* from Santa Barbara,  
448 CA was 496µm. Mean hatching was 1250µm and 1304µm for 2 broods from animals from the  
449 same Santa Barbara population (Collin 2003). The embryos have a large head vesicle which does  
450 not contain yolk and multiple embryonic “kidneys” (see figures in Collin 2000).

451  
452 **Distribution:** From Hotspring Island (52° 35'N; RBCM 979-2392) and Hope Island, British  
453 Columbia (50°54'N; RBCM979-4221) to at least Punta Banda, (LACM 63-42), Todos Santos  
454 (LACM67-45), Boca del Playa (LACM H-532) and Arbolitos (LACM 65320) Baja California,  
455 Mexico in the south. The observed distribution is disjunct with an apparent gap of ~1,000km  
456 between northern CA and the outer coast of WA and the Strait of Juan de Fuca.

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458 **Notes:** See comments for *C. adunca* about past taxonomic confusion between the two species.

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**Discussion**

*Taxonomic misidentifications and phenotypic variation*

Contrary to the historical expectation that *C. norrisiarum* is mostly restricted to southern California, our study shows that the species occurs up to the northern tip of Vancouver Island and in Haida Gwaii. It therefore largely overlaps with the geographic range of its close relative *C. adunca*. We found that the taxonomy of *C. adunca* and *C. norrisiarum* has been consistently confused, especially in the northern part of the range where all small-bodied animals were previously identified as *C. adunca*. Both species occur in the region and the two species are found in sympatry in the outer and transition coasts of the Strait of Juan de Fuca separating BC and WA. To our knowledge, only *C. norrisiarum* is found in the inner, protected waters of Puget Sound, San Juan Islands, and the Gulf Islands, where various aspects of the biology of *C. norrisiarum* have been studied and published under the name “*C. adunca*” (e.g., Hoagland, 1977; Vermeij *et al.*, 1987; Herstoff and Iyengar, 2011; Collin 2000b). For instance, Hoagland (1977) and Vermeij *et al.* (1987) stated that despite extensive dredging in the San Juan Islands, “*C. adunca*” was never found on any other substrate than the shell of other animals, which made that species one of the most specialized slipper limpets in terms of range of substrates occupied. In light of our findings, it appears that this refers to *C. norrisiarum*, which does occur in the San Juan Islands and has not yet been observed attached to rock, while *C. adunca* has been observed attached to rocks at Waddah Island, WA, and Barkley Sound, BC. It seems likely that this taxonomic confusion has also impacted reports of host use. Our revision of published and museum data provide a starting point for more thorough documentation of host use.

484 Results presented here show that shell morphology and body size of *C. adunca* and *C.*  
485 *norrissiarum* are highly variable across their geographic distributions. The ranges in shell shape  
486 and body size largely overlap between the two species and, in both species, size and shape differ  
487 among sampling localities and host use. Therefore, while it seems likely that shell morphology  
488 and body size are host-dependent, it is also possible that phenotypic variation is related to  
489 geographic or bathymetric factors, or that it is the result of genetic differentiation. However, the  
490 shell size of *Crepidula* is necessarily limited by host size (e.g., Pechenik *et al.*, 2020). As a result,  
491 and because subtidal host species are generally larger than intertidal ones, *C. norrissiarum* is twice  
492 as large when living on the large subtidal trochid *Norrisia norrisii* than when living on the small  
493 intertidal trochid *Calliostoma ligatum*. Likewise, *C. adunca* becomes much larger when on the  
494 large subtidal *Tegula pulligo* than on the smaller intertidal *T. funebris*. These observations  
495 support the hypothesis that shell morphology and body size are not species-specific traits but  
496 reflect regional differences in habitat, host use, and host availability.

497

#### 498 ***Geographic distribution, shell museum records, and population genetic structure***

499 Our assessment of museum collections showed that shells of *C. norrissiarum* are relatively  
500 common in southern California, but also occur in parts of central and northern California, the  
501 protected coast of Washington, and the outer and protected coasts of BC. They are, however,  
502 virtually absent from the outer shores of Washington, Oregon, and northern California north of  
503 Marin County. Notably the most common Californian snail hosts, the trochid *N. norrisii* is rarely,  
504 if ever, found north of Point Conception. The very sparse representation in museum collections of  
505 *C. adunca* and other calyptraeids from areas between northern California and the outer coast of  
506 Washington suggests that this exposed stretch of the western coast of the United States has been

507 poorly sampled. On the other hand, this exposed shore may not offer many suitable habitats for  
508 slipper limpets or their hosts. Indeed, numerous studies of intertidal communities in Oregon and  
509 Washington have classified this stretch of shore - dominated by barnacles and mussels and  
510 marked by the Point Conception boundary - as one of the most important biogeographic breaks  
511 on the US west coast (Valentine, 1966; Briggs, 1974; Newman, 1976; Doyle, 1985; Gaylord and  
512 Gaines, 2000), with many widespread northeastern Pacific species being strikingly rare in or  
513 absent from the outer coasts of Washington, Oregon, and northern California (e.g., Kozloff, 2000;  
514 Keever *et al.*, 2009). In spring and summer, strong southward winds along these coasts generate  
515 nearshore upwelling that constitute a strong physical barrier to gene flow in many intertidal  
516 species. For some species, notably those with a pelagic larvae, this biogeographic break is  
517 consistent with a phylogeographic break (e.g., Burton, 1998; Barshis *et al.*, 2011; Wares and  
518 Skoczen, 2019), whereas in other species, this range disjunction does not correspond to any  
519 apparent phylogeographic structure (Keever *et al.*, 2009). For instance, Marko (1998) and Wares  
520 *et al.* (2001) showed that for the direct-developing gastropod species *Nucella emarginata*, these  
521 ocean currents may not represent a physical barrier. Further work is needed to determine the  
522 cause of the apparent disjunct distribution of *C. norrisiarum*, *C. adunca*, and calyptraeids in  
523 general along these shores.

524

525         A noteworthy result of this study is that two sedentary species with direct development  
526 show such large geographic spread with a surprisingly low level of genetic differentiation  
527 between the southern and northern parts of their ranges. Although genetic divergences between  
528 northern and southern populations were highly significant in both species, fixation indexes were  
529 below expected values for other *Crepidula* species lacking dispersal stages. For instance, along  
530 Atlantic coasts of Florida and Yucatan, *C. convexa* and *C. atrasolea*, two direct developers, show



531 extremely high genetic differentiation among localities less than 200 km distant (Collin, 2001).  
532 Although more intense geographical sampling may increase observed  $\Phi_{ST}$  values, the spatial  
533 distribution of haplotypes and the genealogical relationships among them also indicated only  
534 moderate genetic structure between northern and southern regions in both species. Interestingly,  
535 similar population genetic patterns have been observed in other direct developers along the same  
536 shore, like *Nucella ostrina* and *N. lamellosa* (Marko, 2004).

537  
538         Despite our limited sampling, our results can suggest hypotheses for further investigation  
539 when viewed in the context of previous studies on post-glacial range expansions of northeastern  
540 Pacific shallow water species. Studies show that many rocky intertidal species have undergone  
541 large and rapid latitudinal shifts along the northeastern Pacific coast in response to the last glacial  
542 maximum (e.g., Marko *et al.*, 2010; McGovern *et al.*, 2010; Kelly and Palumbi, 2010). In *C.*  
543 *adunca*, the star-shaped haplotype network and the low genetic diversity observed in the northern  
544 region could reflect a recent bottleneck or founder event followed by a demographic expansion of  
545 northern populations. Such genetic patterns were evidenced in similar co-occurring sibling  
546 species (e.g., *Nucella* spp) and attributed to the effects of Pleistocene glaciation, which would  
547 have eliminated northern populations (Marko, 2004). Interestingly, this genetic signature is not  
548 observed in *C. norrisiarum*; despite their close phylogenetic relationship and ecological  
549 similarity, *C. adunca* and *C. norrisiarum* may have contrasting biogeographic histories. Further  
550 sampling of *C. adunca* and *C. norrisiarum* with larger sample size and more genetic markers  
551 enabling robust assessment of past demographic processes (e.g., Marko *et al.*, 2010; McGovern *et*  
552 *al.*, 2010), as well as in-depth comparisons of genetic diversity across host-use and between the  
553 intertidal and subtidal species, are needed to further understand the eco-evolutive  
554 phylogeographic history of these sibling species.

555

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574 **Ethical Care**

575 All material has been collected under appropriate collection permits and threatened in compliance  
576 with approved ethics guidelines.

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705



**Table 1:** List of individuals of *Crepidula adunca* and *Crepidula norrisiarum* analyzed on *cox1* gene.

Locality	GenBank # or BOLD#	Museum voucher #	Depth	Host	Study
<i>C. adunca</i>					
Port Hardy, Vancouver Island	MT048416 = SGPBS011-20	RBCM 012-00012-007	intertidal	no data	Castelin <i>et al.</i> 2016
Quatsino Sound, Strathcona, Vancouver Island	KX069527 = CAMIB070-16	RBCM 016-00194-001	10 m	no data	Castelin <i>et al.</i> 2016
	KX069525 = CAMIB017-16	RBCM 016-00194-004	10 m	no data	Castelin <i>et al.</i> 2016
Brooks Bay, Brooks Peninsula, Vancouver Island	KX069528 = CAMIB062-16	RBCM 016-00195-001	10 m	no data	Castelin <i>et al.</i> 2016
	KX069529 = CAMIB061-16	RBCM 016-00195-002	10 m	no data	Castelin <i>et al.</i> 2016
	KX069519 = CAMIB035-16	RBCM 016-00196-001	10 m	no data	Castelin <i>et al.</i> 2016
	KX069520 = CAMIB034-16	RBCM 016-00196-002	10 m	no data	Castelin <i>et al.</i> 2016
Little Beach, Ucluelet, Vancouver Island	OK526437	LACM 2015-23.1	intertidal	on <i>Nucella lamellosa</i>	This Study
	OK526438	LACM 2014-38.1	intertidal	on <i>Tegula funebris</i>	This Study
	OK526439	LACM 2014-38.2	intertidal	on <i>Tegula funebris</i>	This Study
	OK526440	LACM 2014-38.3	intertidal	on <i>Tegula funebris</i>	This Study
	OK526441	LACM 2014-38.4	intertidal	on <i>Tegula funebris</i>	This Study
	OK526442	LACM 2014-38.5	intertidal	on <i>Tegula funebris</i>	This Study
	OK526443	LACM 2014-38.6	intertidal	on <i>Tegula funebris</i>	This Study
Big Beach, Ucluelet, Vancouver Island	MN992959 = SGPBS001-20	RBCM 016-00197-001	intertidal	on <i>Tegula funebris</i>	Castelin <i>et al.</i> 2016
	MN992958 = SGPBS002-20	RBCM 016-00197-002	intertidal	on <i>Tegula funebris</i>	Castelin <i>et al.</i> 2016
	MN992954 = SGPBS003-20	RBCM 016-00199-001	intertidal	on <i>Tegula funebris</i>	Castelin <i>et al.</i> 2016
	MN992955 = SGPBS004-20	RBCM 016-00199-002	intertidal	on <i>Tegula funebris</i>	Castelin <i>et al.</i> 2016
	MN992956 = SGPBS005-20	RBCM 016-00199-004	intertidal	on <i>Tegula funebris</i>	Castelin <i>et al.</i> 2016
	MN992952 = SGPBS006-20	RBCM 016-00199-005	intertidal	on <i>Tegula funebris</i>	Castelin <i>et al.</i> 2016
	MN992960 = SGPBS007-20	RBCM 016-00199-007	intertidal	on <i>Tegula funebris</i>	Castelin <i>et al.</i> 2016
	MN992957 = SGPBS008-20	RBCM 016-00199-008	intertidal	on <i>Tegula funebris</i>	Castelin <i>et al.</i> 2016
	MN992961 = SGPBS009-20	RBCM 016-00199-009	intertidal	on <i>Lirabuccinum dirum</i>	Castelin <i>et al.</i> 2016
	MN992953 = SGPBS010-20	RBCM 016-00199-011	intertidal	on <i>Lirabuccinum dirum</i>	Castelin <i>et al.</i> 2016
Ucluelet, Vancouver Island	OK526444	LACM 2014-36.1	intertidal	on <i>Tegula funebris</i>	This Study
	OK526445	LACM 2014-36.2	intertidal	on <i>Tegula funebris</i>	This Study
Botanical Beach, Port Renfrew, Vancouver Island	KX069514 = CAMIB419-16	RBCM 016-00191-001	10 m	no data	Castelin <i>et al.</i> 2016
	KX069515 = CAMIB418-16	RBCM 016-00191-002	10 m	no data	Castelin <i>et al.</i> 2016
	KX069516 = CAMIB417-16	RBCM 016-00191-003	10 m	no data	Castelin <i>et al.</i> 2016

	KX069517 = CAMIB416-16	RBCM 016-00191-004	10 m	no data	Castelin <i>et al.</i> 2016
	KX069518 = CAMIB415-16	RBCM 016-00191-005	10 m	no data	Castelin <i>et al.</i> 2016
	KX069526 = CAMIB414-16	RBCM 016-00191-006	10 m	no data	Castelin <i>et al.</i> 2016
Botany Bay, Port Renfrew, Vancouver Island	KX070351 = CAMIB355-16	RBCM 016-00190-002	10 m	no data	Castelin <i>et al.</i> 2016
	KX069523 = CAMIB354-16	RBCM 016-00190-003	10 m	no data	Castelin <i>et al.</i> 2016
	KX070349 = CAMIB353-16	RBCM 016-00190-004	10 m	no data	Castelin <i>et al.</i> 2016
	KX069521 = CAMIB330-16	RBCM 016-00191-007	10 m	no data	Castelin <i>et al.</i> 2016
Cape Alava, Clallam County, Washington	OK526446	LACM 2014-37.1	intertidal	on <i>Tegula funebris</i>	This Study
	OK526447	LACM 2014-37.2	intertidal	on <i>Tegula funebris</i>	This Study
	OK526448	LACM 2014-37.3	intertidal	on <i>Tegula funebris</i>	This Study
	OK526449	LACM 2014-39.1	intertidal	on <i>Tegula funebris</i>	This Study
San Simeon, San Luis Obispo, California	OK526450	LACM 2013-91.1	intertidal	on <i>Tegula funebris</i>	This Study
	OK526451	LACM 2013-91.2	intertidal	on <i>Tegula funebris</i>	This Study
	OK526452	LACM 2013-91.3	intertidal	on <i>Tegula funebris</i>	This Study
	OK526453	LACM 2013-91.4	intertidal	on <i>Tegula funebris</i>	This Study
	OK526454	LACM 2013-91.5	intertidal	on <i>Tegula funebris</i>	This Study
	OK526455	LACM 2013-91.6	intertidal	on <i>Tegula funebris</i>	This Study
	OK526456	LACM 2013-91.7	intertidal	on <i>Tegula funebris</i>	This Study
	OK526457	LACM 2013-91.8	intertidal	on <i>Tegula funebris</i>	This Study
<b><i>C. norrisiarum</i></b>					
Brooks Bay, Brooks Peninsula, Vancouver Island	KX069535 = CAMIB060-16	RBCM 016-00195-003	10 m	no data	Castelin <i>et al.</i> 2016
	KX069530 = CAMIB033-16	RBCM 016-00196-003	10 m	no data	Castelin <i>et al.</i> 2016
Frank Island, Tofino, Vancouver Island	KX070355 = CAMIB474-16	RBCM 016-00189-002	10 m	no data	Castelin <i>et al.</i> 2016
	KX069533 = CAMIB473-16	RBCM 016-00189-003	10 m	no data	Castelin <i>et al.</i> 2016
	KX070357 = CAMIB286-16	RBCM 016-00189-004	10 m	no data	Castelin <i>et al.</i> 2016
	KX070358 = CAMIB285-16	RBCM 016-00189-005	10 m	no data	Castelin <i>et al.</i> 2016
	KX069531 = CAMIB241-16	RBCM 016-00189-006	10 m	no data	Castelin <i>et al.</i> 2016
	KX069537 = CAMIB237-16	RBCM 016-00189-010	10 m	no data	Castelin <i>et al.</i> 2016
Hyphocus Island, Ucluelet, Vancouver Island	OK526458	LACM 2016-16.1	10 m	on <i>Tegula pulligo</i>	This Study
	OK526459	LACM 2016-16.3	10 m	on <i>Tegula pulligo</i>	This Study
Dead Man's Bay, San Juan Island, Washington	AF546047	FMNH282185	intertidal	on <i>Calliostoma ligatum</i>	Collin (2003b)
Yellow Banks, Santa Cruz Island, California	OK526460	LACM 2014-34.1	subtidal	on <i>Norrisia norrisii</i>	This Study
	OK526461	LACM 2014-34.2	subtidal	on <i>Norrisia norrisii</i>	This Study
	OK526462	LACM 2014-34.3	subtidal	on <i>Norrisia norrisii</i>	This Study

	OK526463	LACM 2014-34.4	subtidal	on <i>Norrisia norrisii</i>	This Study
	OK526464	LACM 2014-34.5	subtidal	on <i>Norrisia norrisii</i>	This Study
	OK526465	LACM 2014-34.6	subtidal	on <i>Norrisia norrisii</i>	This Study
	OK526466	LACM 2014-34.7	subtidal	on <i>Norrisia norrisii</i>	This Study
Off Santa Rosa Island, Santa Barbara Co., California	OK526467	LACM 2014-35.1	subtidal	on <i>Norrisia norrisii</i>	This Study
Santa Barbara, California	AF550487	FMNH282173	subtidal	on <i>Norrisia norrisii</i>	Collin (2003a)

**Table 2:** Summary statistics for polymorphism at the *cox1* gene of 657 bp for each analyzed region within each species. N, number of sequences; Nh, number of haplotypes, S, number of segregating sites;  $\pi$ , nucleotide diversity (mean number of pairwise differences); Hd, haplotype diversity with standard deviation (S.D).

Localities	Nh	S	$\pi$ S.D.	Hd S.D.
<i>Crepidula adunca</i>				
Northeastern Pacific Ocean N = 40	4	4	0.2 +/- 0.28	0.146 +/- 0.07
Southeastern Pacific Ocean N = 8	5	6	2.071 +/- 1.47	0.857 +/- 0.10
<i>Crepidula norrisiarum</i>				
Northeastern Pacific Ocean N = 12	7	9	1.681 +/- 1.19	0.833 +/- 0.1
Southeastern Pacific Ocean N = 8	6	6	2.214 +/- 1.55	0.892 +/- 0.11

**Table 3:** List of the hosts associated with *Crepidula adunca* (Ca) and *Crepidula norrisiarum* (Cn). Host geographic range (AK, Alaska; BC, British Columbia; WA, Washington; OR, Oregon; CA, California). Host/Substrate on which *Ca* or *Cn* was found with location (north, N [from Alaska to Oregon]; south, S [along California State]) where association was found. List of sources for which association was personally confirmed and *Crepidula* species identity unambiguous.

Host range	Host/Substrate	Ca	Cn	Reference
	<i>On rocks</i>	N		R.H. pers. obs. Waddah Island, Neah Bay, WA, RBCM21-53-1; J.H. McLean, Barkley Sound, BC, LACM 26030
AK to CA	<i>Tegula funebris</i>	N, S	S	<i>Ca</i> : LACM R-343; LACM 161708; CAS 231214; R.H. pers. obs. Ucluelet, BC; Putnam 1964 / <i>Cn</i> : CAS 55598
AK to CA	<i>Tegula pulligo</i>	N	N,S	<i>Ca</i> : RBCM 979-9595 / <i>Cn</i> : R.H. pers. obs. Ucluelet, BC; Monterey, CA, LACM 60-24.
AK to CA	<i>Lirabuccinum dirum</i>	N		R.H. pers. obs. Ucluelet, BC; Clover Pt., Victoria, BC; L. Schroeder pers. obs. Salt Creek County Park, W of Port Angeles, WA; N. Treneman, pers. obs. Cape Arago, OR.
AK to CA	<i>Amphissa columbiana</i>	N		R.H. pers. obs.; Ucluelet, BC; Vermeij et al. 1987.
AK to CA	<i>Nucella lamellosa</i>	N		R.H. pers. obs.; Ucluelet, BC; Victoria, BC; Slip Pt., Strait of Juan de Fuca, WA; Clover Pt. Victoria
AK to CA	<i>Calliostoma ligatum</i>	N	N	<i>Ca</i> : R.H. Ucluelet, BC; both <i>Ca</i> and <i>Cn</i> in the same sample RBCM979-4221. RC San Juan Island, WA
BC to CA	<i>Alia carinata</i>	N	S	<i>Ca</i> : R.H. Ucluelet, BC; <i>Cn</i> : MacGinitie and MacGinitie, 1964
AK to WA	<i>Neostylidium eschrichtii</i>	N		R.H. pers. obs. Ucluelet, BC
AK to CA	<i>Pseudodiala acuta</i>	N		R.H. pers. obs. Ucluelet, BC
AK to CA	<i>Pomaulax gibberosus</i>	N		R.H. pers. obs. Ucluelet, BC
	<i>Homalopoma sp.</i>	N		R.H. pers. obs. Ucluelet, BC
AK to CA	<i>Philobrya setosa</i>	N		R.H. pers. obs. Ucluelet, BC
CA	<i>Tegula gallina</i>	S		LACM 161700
CA	<i>Tegula montereyi</i>	S		R.C. pers. obs. Diablo Canyon, CA
OR to CA	<i>Tegula brunnea</i>	S		S. Lonhart, Monterey Co., California; N. Treneman Crescent City, CA 6-7-2019
CA	<i>Atrimitra idae</i>	S		LACM 161700; R.C. pers. obs. Diablo Canyon, CA
CA	<i>Acanthinucella paucilirata</i>	S		C.A. Clark record (iNaturalist 19263592) Princeton-by-the Sea, CA.

CA	<i>Norrisia norrisii</i>	S	Warner et al. 1996; Hobday et al. 1998; MacGinitie & MacGinitie 1964; R.C. pers. obs.; LACM 60278; LACM161798; FMNH 282173-175.
	<i>Haliotis spp.</i>	S	LACM 19435; Smith, 1946
BC to CA	<i>Haliotis rufescens</i>	S	CAS231212
AK to CA	<i>Nassarius mendicus (N. cooperi)</i>	S	MacGinitie and MacGinitie, 1964
AK to CA	<i>Randallia bulligera</i> (crab)	S	MacGinitie and MacGinitie, 1964
AK to CA	<i>Calliostoma canaliculatum</i>	S	Hazard Conyon, S of Morro Bay, CA
	<i>Calliostoma sp.</i>	S	CAS231213
OR to CA	<i>Tegula brunnea</i>	S	CAS231215; D.E. pers. obs. from San Luis Obispo and Monterey Counties, CA
CA	<i>Tegula eisini</i>	S	Alex Baristow, La Jolla, CA (iNaturalist 9652706)

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## Figure legends

**Figure. 1:** Map of the northeastern Pacific coast with magnification of sample localities of *Crepidula adunca* and *C. norrisiarum* from British Columbia and Washington State (A) and from California (B). Numbers on the map correspond to sample size per locality and per species.

**Figure. 2:** Median-joining network obtained from *cox1* sequences of *Crepidula adunca* in British Columbia and Washington State (A) and California (B). Circles are color coded based on sampling location and are sized according to the relative abundance of each haplotype. Each line connecting a circle or a small bar equals one mutational step.

**Figure. 3:** Median-joining network obtained from *cox1* sequences of *Crepidula norrisiarum* in British Columbia and Washington State (A) and California (B). Circles are color coded based on sampling location and are sized according to the relative abundance of each haplotype. Each line connecting a circle or a small bar equals one mutational step.

**Figure. 4:** The Holotype of *Crepidula adunca* Sowerby, 1825 (NHMUK 1997150) with arrow pointing out the dimple. Scale = 1 cm. © The Trustees of the Natural History Museum. Images by Phil Hurst, NHMUK Photographic Unit.

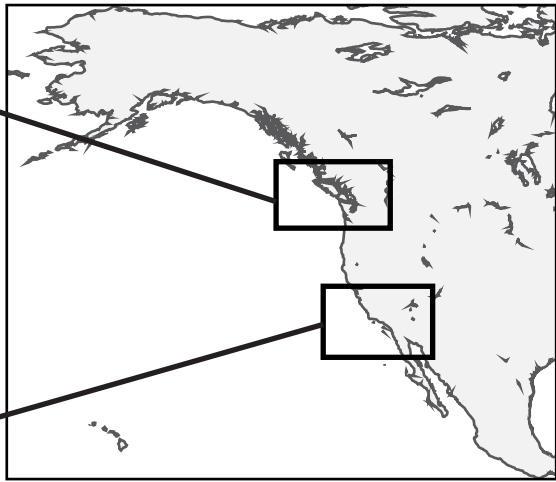
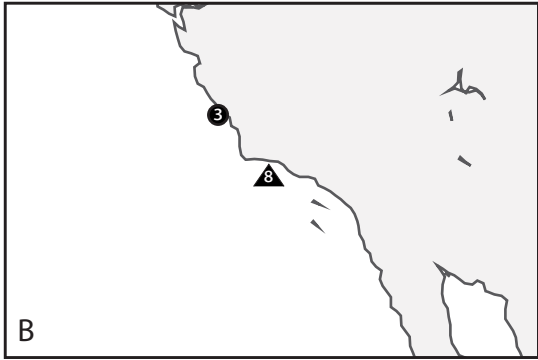
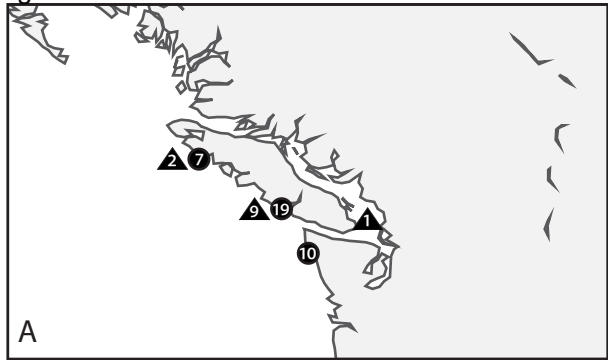
**Figure. 5:** Shells of *Crepidula norrisiarum*. (A) *C. norrisiarum* (LACM 182442) collected from *Calliostoma ligatum* on San Juan Island, Washington and (B) *C. norrisiarum* (LACM 182441) collected from *Norrisia norrisii* from Naples Reef near Santa Barbara, California (Photos by Maycol Maycol E. Madrid C.).

**Figure. 6:** Live *Crepidula norrisiarum* (A) and *C. adunca* (B) showing the difference in body color.

**Figure. 7:** *Crepidula adunca* and *C. norrisiarum* on different hosts. (A). *Crepidula adunca* on *Lirabuccinum dirum* from south Cove, Cape Arago, Oregon (Photo by: Nancy Treneman). (B)

*Crepidula adunca* on *Tegula montereyi* from Monterey Co., California (Photo by Steve Lonhart)  
(C) *Crepidula adunca* on *Pomaulax gibberosus* from Ucluelet, British Columbia. (D) *Crepidula norrisiarum* on *Norrisia norrisi* from Los Angeles Co., California. (E) *Crepidula adunca* on *Tegula funebris*. (F) *Crepidula norrisiarum* on *Calliostoma ligatum* from Keystone, Whidbey Island, WA (Photo by: Jan Kocian) (G) *Crepidula norrisiarum* on *Calliostoma ligatum* from Victoria, BC (Photo by: James Hester).

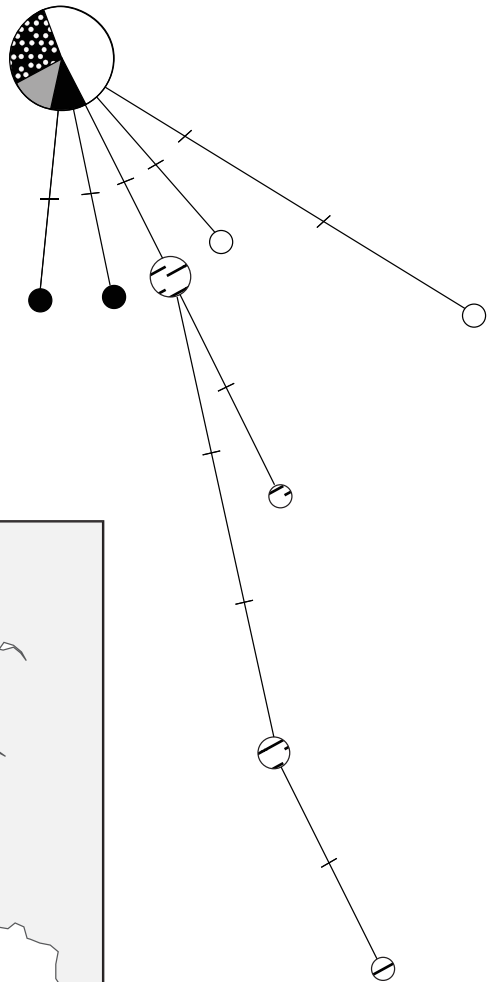
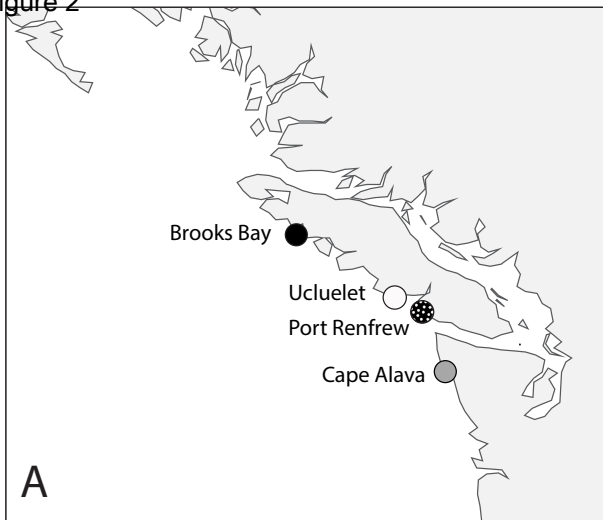
Figure 1



- *Crepidula adunca*
- ▲ *Crepidula norrisiarum*

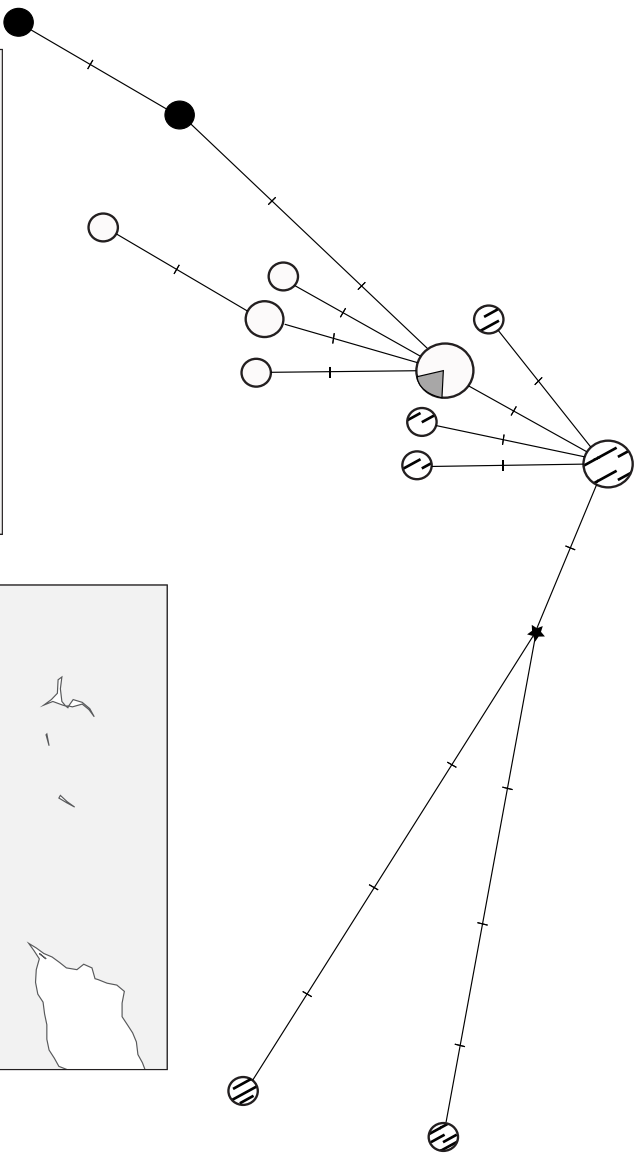
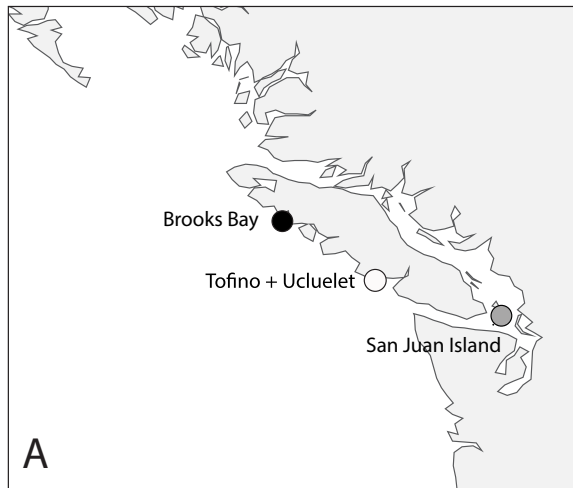


Figure 2



*Crepidula adunca*

Figure 3



*Crepidula norrisiarum*



**A**

4mm

**B**

1cm

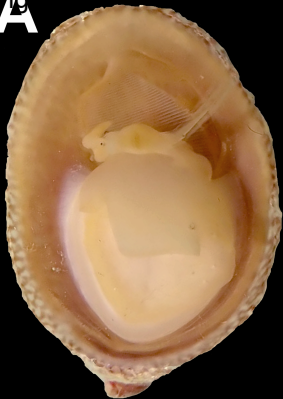
**A****B**

Figure 7

