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THE LAST KNOWN *ENDODONTA* SPECIES? *ENDODONTA CHRISTENSENI* SP. NOV. (GASTROPODA: ENDODONTIDAE)

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Cover photo: *Endodonta christenseni* Slapcinsky, Yeung & Hayes from Nihoa. Photo: David Sicscho.

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The last known *Endodonta* species? *Endodonta christenseni* sp. nov. (Gastropoda: Endodontidae)[1]

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Abstract. The Endodontidae are land snails endemic to Pacific islands, and the type genus *Endodonta* and its 11 species are endemic to the Hawaiian Archipelago. Most members of the family, because of their ground dwelling habits, are vulnerable to introduced predators and most of the species in Hawaii are already extinct. Fossil specimens have been used to describe extinct species, but no living *Endodonta* species have been described in more than 100 years. Over the last 15 years, the most comprehensive search for land snails in Hawaii has been carried out, with more than 1000 sites surveyed to date. The only known living *Endodonta* species is from the island of Nihoa, discovered in 1923, but remaining undescribed until now. Here we finally give what we think is the last *Endodonta* species a name and describe it using an integrative taxonomic approach. In describing this last *Endodonta* species, our hope is to inspire increased awareness and appreciation that facilitates and motivates conservation for this species and all the other undiscovered and unnamed species threatened with extinction. Unless protection of this species is implemented, it may be extinct within the next decade and we will lose the last of a lineage that existed for millions of years, and the stories it could tell.

Keywords: extinction, gastropod, mollusc, Pacific islands, invertebrate conservation

INTRODUCTION

The Endodontidae Pilsbry, 1895 is a diverse family of land snails endemic to Pacific islands and restricted to Polynesia, Palau, and Fiji's Lau Archipelago (Solem 1976, 1990). The type genus of the family is *Endodonta* Albers, 1850 and all 11 species are endemic to the Hawaiian archipelago (Solem 1976, Cowie *et al*. 1995). Solem (1990) concluded that all low and mid-

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[1] Contribution No. 2020-012 to the Hawaii Biological Survey.

elevation endodontid species, including all described *Endodonta* species, were extinct in the main Hawaiian Islands by 1960 and the remaining (< 5%) were confined to high elevation refugia. Both species of *Endodonta* described since 1960, *E. ekahanuiensis* Solem, 1976 and *E. kalaeloana* Christensen, 1982 were extinct at the time of their description. As such, no living *Endodonta* species has been described since Pilsbry & Vanatta (1905).

Although there have been many surveys for land snails in the Hawaiian archipelago over the last century and half, our team along with collaborators began intensive and broad scale surveys for native and non-native land snails in Hawaiʻi in 2004. Over that time, more than 1,000 sites have been surveyed to document the remaining terrestrial gastropods in Hawaiʻi. No live *Endodonta* species were recorded from the main Hawaiian Islands and the only extant *Endodonta* known is an undescribed species from the island of Nihoa, located approximately 250 km northwest of Kauaʻi. This species was discovered by C.M. Cooke, Jr. and D. Thaanum in 1923, and recollected a year later by E.H. Bryan, Jr. and T.T. Dranga in the course of biological surveys of the Northwestern Hawaiian Islands during the *Tanager* Expedition, conducted by the Bernice P. Bishop Museum (BPBM) in partnership with the United States Bureau of Biological Survey. This species was not reported again until 1980 by Carl Christensen and reported by Conant *et al*. (1984); and was later collected by BPBM entomologist John Strazanac in 1990 (BPBM 251225, 251233).

Although it has been nearly a century since its discovery, this species has remained unnamed. Here we describe the only known remaining extant *Endodonta* species, *Endodonta christenseni* sp. nov. Giving this species a name is the first step to putting it on track for conservation, and we hope that in doing so, it and other Hawaiian land snails will begin to receive the increased management resources needed to conserve them in the face of the ongoing biodiversity crisis.

MATERIAL AND METHODS

Land snail surveys were conducted by DRS on Nihoa Island 5–8 Jun 2015 in conjunction with yearly monitoring of bird and plant species by the Pacific Islands Fish and Wildlife Service. Spot surveys along transect lines, from sea level to the island's summits, were searched for snails at intervals of approximately 20 m. In previous surveys, snails were located primarily in clumps of the grass *Eragrostis variabilis* (Gaud.) Steud. (Fig. 1). Therefore, transect surveys targeted portions of the island with high abundance of this grass. Parts of Nihoa still support remnant groves of *Pritchardia remota* Becc. Palm species in this genus are important host plants for snail species in the main Hawaiian Islands. As such, survey efforts were also focused on portions of the island with high palm cover.

Transect surveys took the path of least resistance, altering routes to avoid disturbance to nesting seabirds, rare plants, and cultural sites. When snails were discovered along a transect line a more thorough survey was conducted in an approximately 10 m × 10 m quadrat. If snail abundance was high (> 50 individuals observed within a quadrat) three voucher specimens were collected for morphological and genetic analyses. These vouchers were selected to encompass the range of morphological variation observed at each site.

All live specimens collected were heat-shocked (Fukuda *et al*. 2008) and preserved in 95% EtOH for transport to the Malacology Department at BPBM for identification via morphological and genetic analysis, and for long-term preservation. Voucher specimens are housed at BPBM, Honolulu, (BPBM 286681–286689) and the Florida Museum of

Figure 1. Photographs of *Eragrostis variabilis* on Nihoa where *Endodonta christenseni* sp. nov. was found. Photos: D.R. Sischo.

Natural History, Gainesville (UF 563514, 563518, 563523, 563526). All catalog numbers indicated below are BPBM, except where noted as UF. Permit requirements precluded listing the exact locality data here for conservation purposes but they are kept in the State of Hawaiʻi Department of Land and Natural Resources Snail Extinction Prevention Program and BPBM Malacology databases and are available on request with approval.

Shells and reproductive anatomy were photographed with a digital single-lens reflex camera (Nikon D90 with 60 mm Nikkor lens). Photographs of reproductive anatomy were traced in Adobe Photoshop and Illustrator (CS6) to produce line drawings. Shell measurements were made using an ocular micrometer and each measurement was repeated three times and averaged for each of 25 adult specimens. Shell measurements – shell height (H), shell width (W), aperture height (AH), aperture width (AW), umbilical width (UW), and number of whorls (WH) were made following Slapcinsky and Coles (2004: p. 56, figs. 1–3). Terminology of teeth follows Solem (1976: p. 52, fig. 36). High-resolution X-ray computed tomography (CT) using the GE Phoenix V|TOME|X M 240 Nano CT scanner at the University of Florida's Nanoscale Research Facility generated 2200 projections of BPBM 286681 (holotype). X-ray acquisition specifications were 70 kV, 85 µA, exposure 0.250097 s with frame averaging of 3. Radiographs were reconstructed to tomograms with a voxel resolution of 5.84456 µm using Phoenix Datos|x software (Waygate Technologies, Hürth, Germany), and 3D volumetric analysis performed using VGSTUDIO MAX 3.3 (Volume Graphics, Heidelberg, Germany). Image stacks (TIFF) and 3D mesh files (STL) are deposited in MorphoSource doi:10.17602/M2/M104794.

Radulae were obtained by digesting buccal mass tissue for 15–30 min at 55 °C in 195 µl of T1 lysis buffer (Macherey-Nagel) containing 1.5 µg/µl of Proteinase-K. Following digestion, radulae were rinsed with de-ionized water and mounted directly on carbon adhesive tabs attached to aluminum stubs, which were then coated with 25–30 nm gold/palladium (60/40) and photographed using a Hitachi S-4800 at the Biological Electron Microscope Facility (University of Hawaiʻi at Mānoa).

Genomic DNA (gDNA) was extracted from 21 snails, 17 *Endodonta christenseni* sp. nov. and 4 *Cookeconcha hystricella* (Pfeiffer, 1959), collected on Oʻahu during previous surveys and for captive rearing. An approximately 1 mm^3 piece of foot tissue or in some cases buccal mass tissue used during radulae preparation was digested using the

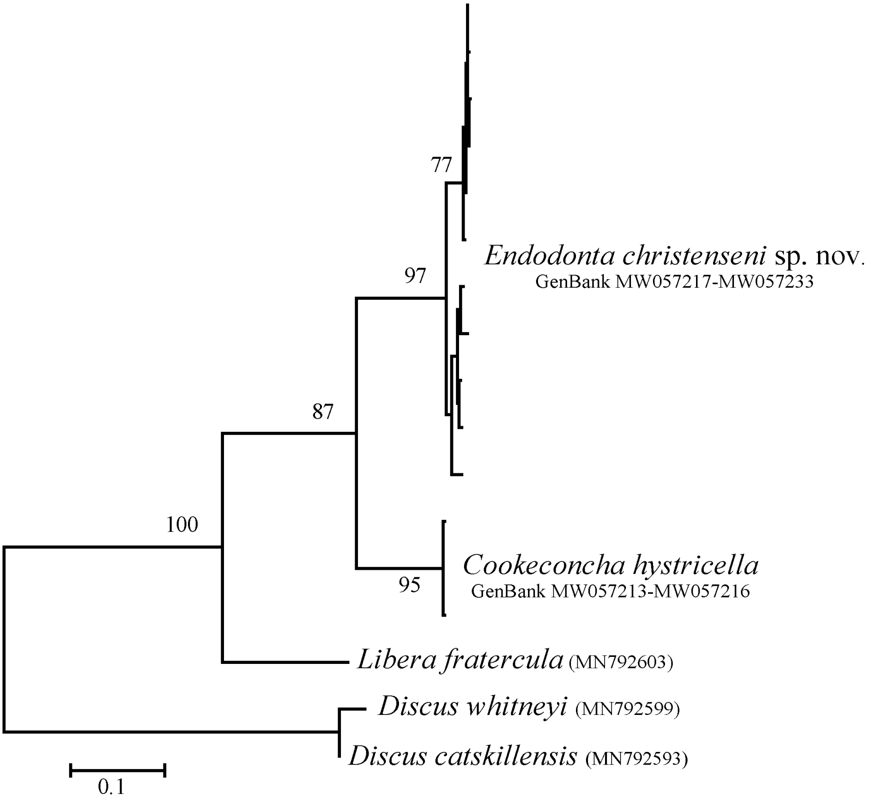

Figure 2. Phylogenetic tree reconstructed using Maximum Likelihood analyses of COI sequences to show the relationship of *Endodonta christenseni* sp. nov. to one other Hawaiian endodontid and closely related taxa represented by sequences on GenBank. Node values represent Ultrafast bootstrap support from 10000 replicates implemented in IQ-TREE.

Macherey-Nagel NucleoSpin® Tissue Kit following the manufacturer's instructions, with the exception that elution was with 60 µl of elution buffer supplied with the kit. Genomic DNA and tissue samples are cryopreserved in the Pacific Center for Molecular Biodiversity at BPBM (*E. christenseni* sp. nov. PCMB 52205–52221; *C. hystricella* BPBM 286746, PCMB 52198, 52199, 52201, 52202). Portions of cytochrome *c* oxidase subunit I (MT-COI), were amplified via the polymerase chain reaction (PCR) using the primers LCO1490/HCO2198 (Folmer et al. 1994). Reactions were carried out in 25 µl volumes containing 1–2 µl template DNA and a final concentration of 1 U of MangoTaq™ DNA polymerase (Bioline), 1X reaction buffer, 0.2 mM each dNTP, 2.5 mM $MgCl_2$, 0.75 µM of each primer, 0.4 µg/µl BSA, and 0.5% DMSO. Cycling parameters consisted of a single cycle of 5 min at 95 °C, 1 min at 45 °C, 1 min at 72 °C, followed by 34 cycles of 95 °C, 48 °C, and 72 °C for 30 s each, and a final extension of 5 min at 72 °C.

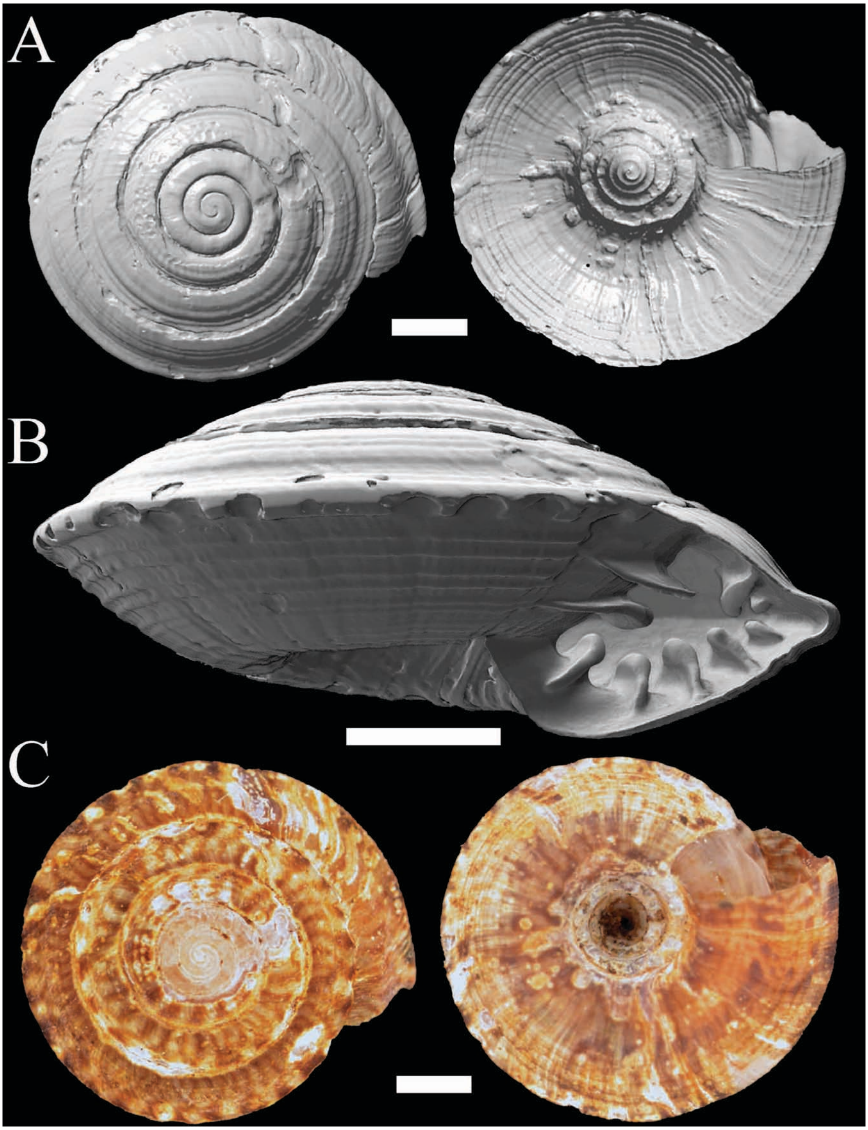

Figure 3. *Endodonta christenseni* sp. nov. **A**) MicroCT images of holotype (BPBM 286681), apical (left) and umbilical (right) views. **B**) MicroCT apertural view. **C**) Color pictures of apical and umbilical views of Holotype (BPBM 286681). Scale bars = 1 mm Photo: J. Slapcinsky.

A final 4 °C incubation of 10 min terminated each reaction. The amount and specificity of amplifications were verified via agarose gel electrophoresis and single product amplicons were cycle sequenced using an ABI BigDye terminator kits (Perkin-Elmer Applied

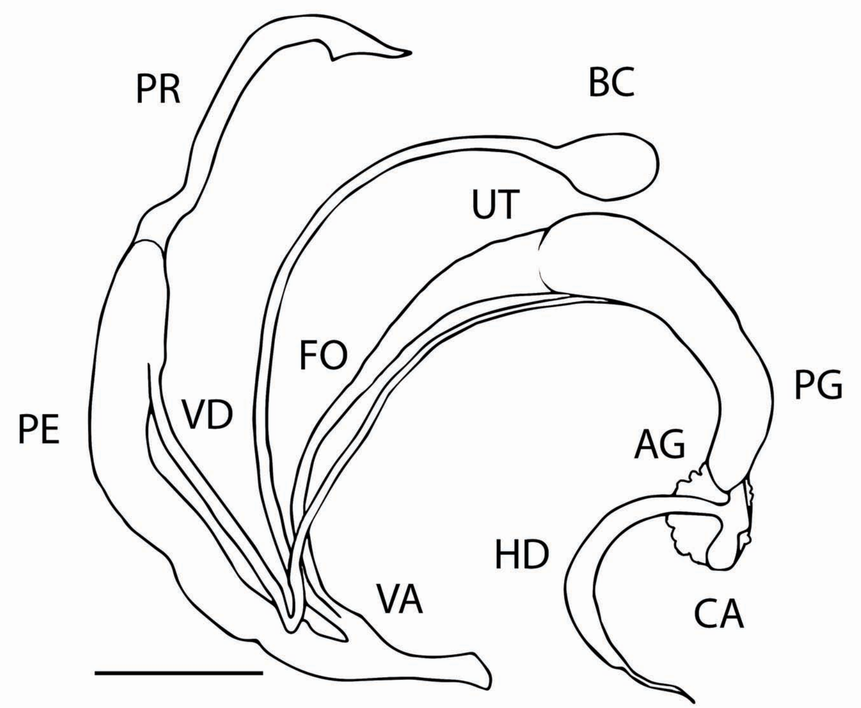

Figure 4. Reproductive anatomy of *Endodonta christenseni* sp. nov. paratype (BPBM 286689). Abbreviations for reproductive structures: AG = albumin gland; BC = bursa copulatrix; CA = carrefour; FO = free oviduct; HD = lower hermaphroditic duct; PH = phallus; PG = prostate gland; PR = phallar retractor muscle; UT = uterus; VA = vagina; VD = vas deferens. Scale bar = 1 mm. Illustration: J. Slapcinsky.

Biosystems, Inc., Waltham, Massachusetts). Sequences were electrophoresed and analyzed on an ABI 3730XL (Perkin-Elmer Applied Biosystems, Inc.) at Eurofins Genomics, LLC, Louisville, Kentucky. All loci were initially sequenced in one direction, and any unique haplotypes sequenced in the other direction to produce full contigs. All sequences have been uploaded to the BarCode of Life Database (BoLD) and to GenBank (Accession numbers MW057213-MW057233).

Electropherograms were checked for errors, edited and assembled using Geneious Prime 2020.2.2 (http://www.geneious.com). Sequences of COI generated as part of this study and two Discidae, *Discus whitneyi* (Newcomb, 1864) and *Discus catskillensis* (Pilsbry, 1896), from the northeastern US, and one Endodontidae, *Libera fratercula* (Pease, 1867), from the Cook Islands. The COI sequences downloaded from GenBank were unambiguously aligned using MAFFT ver. 7.388 with the iterative refinement method E-INS-I (Katoh & Standley 2013) implemented in Geneious Prime. Alignments where checked against amino acid sequences as references to verify an open reading frame and then exported as PHYLIP files for phylogenetic analysis.

Phylogenetic reconstruction was conducted using maximum likelihood (ML) in IQ-TREE ver. 1.6.12 (Nguyen *et al.* 2015). The best-fit partitioning scheme and the most appropriate substitution model for each partition were estimated using the integrated ModelFinder algorithm (Kalyaanamoorthy *et al.* 2017) and partition models (Chernomor *et al*. 2016). Nodal support was estimated with 10,000 ultra-fast bootstrap replicates (Hoang *et al*. 2018). Genetic distances were calculated using a K2P model implemented in MEGA 10.1.7 (Kumar *et al.* 2018).

RESULTS

Endodonta christenseni sp. nov. was recorded at 9 sites across Nihoa from 139 m to 289 m in elevation. In all instances, they were found in clumps of *Eragrostis variabilis*, predominantly inhabiting the lower center portion of the plants where conditions probably remain cooler and wetter than the surrounding area. No *Endodonta* sp. or other snail species previously recorded from Nihoa (i.e. *Philopoa singularis* Cooke & Kondo 1960*, Tornatellides* spp.), were observed on *Pritchardia remota*.

The 17 *Endodonta christenseni* sp. nov. and 4 *Cookeconcha hystricella* that were sequenced produced 11 and 3 COI haplotypes, respectively. Alignment of these newly generated sequences with two sequences from outgroup taxa from GenBank produced an alignment matrix of 655 bp with 465 invariant and 152 parsimony informative sites. The best fit model determined by ModelFinder was HKY+F+I according to the Bayesian Information Criterion. The ML tree (Fig. 2) recovered the two Hawaiian species as reciprocally monophyletic sister taxa in a clade sister to *Libera fratercula*. The mean genetic distance (K2P) was 0.002 and 0.023 within *Cookeconcha hystricella* and *Endodonta christenseni* sp. nov., respectively, while the two taxa differed by an average of 0.120 (K2P). The mean genetic distance between *Libera fratercula* and the two Hawaiian taxa was 0.177.

SYSTEMATICS

Stylommatophora A. Schmidt, 1855
Endodontidae Pilsbry, 1895
Endodonta Albers, 1850

Endodonta christenseni Slapcinsky, Yeung & Hayes **sp. nov.**
(Figs. 3–6)

Holotype. H = 2.3 mm, W = 5.3 mm, AH = 1.3 mm, AW =2.0 mm, UW = 1.4 mm, WH = 5.8 whorls; GenBank: MW057222BPBM 286681.

Type locality. USA, Hawai‘i, Northwestern Hawaiian Islands, Nihoa Island, near Miller’s Peak, D.R. Sischo, 5 Jun 2015, hand collected in base of *Eragrostis variabilis*.

Paratypes. USA, Hawai‘i, Northwestern Hawaiian Islands, Nihoa Island • 20; same locality as for holotype; 6 Jun 2015; same collector as for holotype; same collection method and habitat as for holotype; 286682, UF 563518 • 2; same locality as for preceding; same collector as for preceding; same collection date as for preceding; same collection method and habitat as for preceding; 286684 • 8; Miller’s Peak; same collector as for preceding; same collection date as for preceding; same collection method and habitat as for preceding; 286683 • 1; mid ridge between Miller’s Peak and Tanager Peak; same collector as for preceding; same collection date as for preceding; same collection method and habitat as for preceding; 286685 • 7; same locality as for preceding; same collector as for preceding; same collection date as for preceding; same collection method and habitat as for preceding;

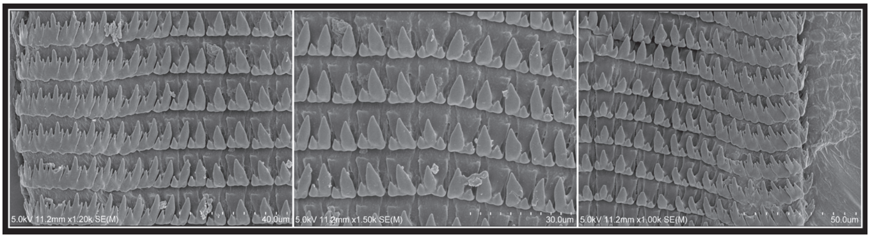

Figure 5. Radula of *Endodonta christenseni* sp. nov. (BPBM 286681) Photos: N.W. Yeung.

286686, UF 563523 • 2; east of Miller's Peak; same collector as for preceding; same collection date as for preceding; same collection method and habitat as for preceding; 286687 • 3; lower Tanager Peak; same collector as for preceding; same collection date as for preceding; same collection method and habitat as for preceding; 286688 • 20; Tanager Peak; same collector as for preceding; 8 Jun 2015; same collection method and habitat as for preceding; 286689, UF 563514.

Other (non-type) material examined. USA, Hawai'i, Northwestern Hawaiian Islands, Nihoa Island – Honolulu County, Oahu, Koolau Mountains • 3; Valley 2 under Wilder's Rock 1/3 mi. from shore; 11 Jun 1923; D. Thaanum; 57138 • 1; Valley 2 hillside near top of valley 1/3 mi. from shore; same collection date as for preceding; C.M. Cooke, Jr., D. Thaanum; 57143 • 11; Valley 2 W. hillside 1/3 mi. from shore; same collection date as for preceding; same collectors as for preceding; 57149 • 10; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57156 • 7; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57167 • 98; Valleys 5 and 6 ridge at bottom of valley 200 yds from shore; 12 Jun 1923; C.M. Cooke, Jr.; 57202 • 1; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 57203 • 247; Valley 6, at head; same collection date as for preceding; D. Thaanum; 54509 • 203; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 57216 • 1; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 57217 • 1; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 57218 • 204; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 0 • 4; ; same collection date as for preceding; E.H. Bryan, Jr.; 57397 • 38; Flat N. of highest peak; 13 Jun 1923; C.M. Cooke, Jr., D. Thaanum; 54530 • 297; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57273 • 7; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57274 • 20; Valley 3 W ridge; same collection date as for preceding; same collectors as for preceding; 57223 • 23; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57224 • 154; Ridge between 2 and 3; same collection date as for preceding; same collectors as for preceding; 57241 • 2; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57242 • 274; Valleys 2 and 3, highest peak between; same collection date as for preceding; same collectors as for preceding; 57257 • 6; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57258 • 2; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57259 • 40; Valley 2, top of W. ridge at Wilder's rock; 14 Jun 1923; same collectors as for preceding; 57284 • 107; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57285 • 94; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57287 • 106; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 0 • 47; N. slope and branch, near top of W. ridge; same collection date as for preceding; D. Thaanum; 57307 • 5; Extreme W. ridge, S. slope; same collection date as for preceding; same collector as for preceding; 57318 • 187; Valley 7 near top of valley;

Figure 6. Live snails found on dry stems and leaves in clumps of *Eragrostis variabilis* Scale Bars = 2 mm. Photos: D.R. Sischo.

15 Jun 1923; C.M. Cooke, Jr., D. Thaanum; 57361 • 26; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57362 • 2; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57363 • 94; E. ridge Valley 7; same collection date as for preceding; same collectors as for preceding; 57382 • 18; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57383 • 19; same locality as for preceding; same collection date as for preceding; same collectors as for preceding; 57384 • 68; Miller's Pk; 10 Jul 1924; T.T. Dranga; 77749 • 72; Valley above Adams Bay W side of Val. #3; same collection date as for preceding; same collector as for preceding; 77755 • 68; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 77756 • 51; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 77757 • 119; Valley #4 E side; 12 Jul 1924; same collector as for preceding; 77767 • 64; South slope of Miller Peak, about 50 feet below summit; 29 Jun 1980; C.C. Christensen; 207099 • 6; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 207100 • 7; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 207108 • 1; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 207109 • 16; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 0 • 5; South slope of Miller Peak, about 100 feet below summit; same collection date as for preceding; same collector as for preceding; 207115 • 2; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 207116 • 2; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 207120 • 18; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 207121 • 3; same local-

ity as for preceding; same collection date as for preceding; same collector as for preceding; 207122 • 7; Below Miller's Peak on ridge to East side of West Palm Valley; same collection date as for preceding; same collector as for preceding; 207127 • 2; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 207134 • 2; same locality as for preceding; same collection date as for preceding; same collector as for preceding; 207135 • 10; East Palm V. west side; 28 Jun 1990; J. Stazanac, Rollen; 251225 • 31; Top of West Palm V. west side; same collection date as for preceding; J. Stazanac; 251233.

Description

Shell

Shell lenticular, H = 2.3 ± 0.13 mm, W = 4.7 ± 0.20 mm, umbilicate, UW = 1.2 ± 0.11 mm, 5.9 ± 0.13 narrow whorls (Fig. 3). Apex dome shaped, first 3 whorls nearly planar, remainder descend gradually. Protoconch smooth. Early teleoconch whorls sculptured with poorly defined, progressively weakening radial ribs as well as progressively strengthening spiral striae becoming cords. After 3.5 whorls, radial ribs disappear leaving 5 spiral cords, central one strongest. Cords until final 1/2 whorl, weakening, replaced by strong growth lines. Shell periphery carinate, strong sulcus above, shallow depression below, rounded cord-like keel. Shell base flattened between keel and umbilicus, bearing paired spiral cords strongest near periphery, fading toward umbilicus. Umbilicus slightly more than one-fourth shell width, steep flattened sides and rounded bottom.

Shell aperture trapezoidal, AH = 1.3 ± 0.06 mm, AW = 1.9 ± 0.08 mm, opening obstructed by 7–10 lamellar barriers (Fig. 3). Two parietal lamellae occupy final 1/3 whorl emerging slightly beyond shell opening. Upper parietal lamella simple at aperture, widening, indistinctly bifid abaperturally. Lower parietal thickened, turned slightly downward inside the aperture. Columellar and palatal lamellae recessed just behind apertural edge. Large, crescent-shaped columellar lamella emerges from the columella at 90°, terminus thickened and turned slightly upward. Five crescent-shaped, apically thickened palatal lamellae often present, four below shell margin, one above. Second palatal largest, fourth palatal sometimes missing, especially in younger individuals. Additional trace lamellae often present between and slightly behind main palatals, especially between palatals 3-5 as seen just below palatal 5 in Fig. 3. Fifth palatal bent downward almost parallel to shell axis, sinuous terminus thickened and turned upwards.

Shell yellow-brown with red-brown, irregular, maculated lines varying in intensity and coverage (Fig. 3). Protoconch approximately 2.5 whorls, light yellow-brown. Early teleoconch whorls on apical surface bear wide radially oriented red-brown bands approximately same width as interspaces. Bands on subsequent whorls gradually narrow along proximal (apical) suture, maintaining width at the distal (peripheral) suture, connection between distal and proximal sides of bands becoming irregular before severing. Penultimate whorl and body whorl have many closely spaced parallel lines along proximal suture that extend halfway between sutures, shell periphery marked with evenly spaced, large reddish-brown spots. Basal surface maculations less regular, strongest near shell periphery and edge of umbilicus. Middle shell base maculations fuse forming irregular reddish-brown band.

Occasionally, shell nearly uniform dark brown (e.g. UF 563529) or uniformly yellow-brown without maculated lines (e.g. BPBM 57274).

Reproductive system
Lower hermaphroditic duct (HD) thickened, joining shaft of large bulbous carrefour (CA) at right angle (Fig. 4). Albumen gland (AG) small, comprised of large, loosely packed acini. Prostate gland (PG) composed of small densely packed ascini. Uterus (UT) long, tapering slowly to narrow free oviduct (FO). Bursa copulatrix (BC) bulbous with long narrow duct nearly equal width as narrow free oviduct. Vagina (VA) short, long as wide, and half width of phallus (PH) where they meet. Vas deferens (VD) sharply bent at penioviducal angle and entering phallus laterally below apex. Phallar retractor muscle (PR) originates from columellar muscle. Phallus cylindrical, apex not significantly expanded, tapering slightly basally. Ovotestis embedded in hepatopancreas (not figured).

Radula
Radula typical of endodontids (Solem 1976). Teeth per row 9-6-1-6-9 (n = 1)Tricuspid central tooth with two symmetric ectocones approximately one third the length of mesocone. Mesocone slightly shorter than mesocone on flanking first lateral teeth. Six bicuspid laterals with ectocones one-third the length of the mesocones. Transition to tricuspid marginals after sixth lateral tooth, tricuspid marginals with weak endocones increasing to approximate size of mesocone towards marginal edge. Ectocones progressively longer marginally (Fig. 5).

Distribution and ecology. *Endodonta christenseni* sp. nov. is endemic to the Northwestern Hawaiian island of Nihoa. The species was locally abundant in the native grass *Eragrostis variabilis* (Fig. 1), in which it was found on the stems and dead leaves at the base of the plants (Fig. 6). No specimens were found on palms, dead twigs or under stones. *Endodonta christenseni* sp. nov. has not been observed carrying its eggs in the umbilicus as reported for *E. marsupialis* Pilsbry & Vanatta, 1905 and *E. concentrate* (Pilsbry & Vanatta, 1905), and other endodontid species (Pilsbry & Vanatta 1905).

Remarks. The strong spiral cords on both the shell apex and base of *Endodonta christenseni* sp. nov. differentiate it from the smooth taxa: *E. concentrata, E. kamehameha* Pilsbry & Vanatta, 1905*, E. lamellosa* (Férussac, 1824)*, E. marsupialis* and *E. fricki* (L. Pfeiffer, 1858) as well as from *E. apiculata* Ancey, 1899, which has a smooth apex. The last two whorls of *E. christenseni* sp. nov. do not have the axial ribbing found in *E. ekahanuiensis, E. kalaeloana, E. laminata* (Pease, 1866)*,* and *E. rugata* (Pease, 1866). *Endodonta binaria* (L. Pfeiffer, 1856) is most similar to *E. christenseni* sp. nov. but has stronger radial ribs on its early whorls and weaker striae on its later whorls and its periphery is strongly crenulate, unlike *E. christenseni* sp. nov.

Of the three species of *Endodonta* for which reproductive anatomy is known, *E. christenseni* sp. nov. has a relatively wide and short phallus similar to *E. lamellosa*, and unlike the long narrow phalluses of *E. fricki* or *E. marsupialis.* The base of the phallus is not strongly tapered in *E. christenseni* sp. nov., *E. fricki* or *E. marsupialis* unlike the basally tapering phallus of *E. lamellosa*. The uterus of *E. christenseni* sp. nov. tapers gently and the free oviduct is shorter than that of any of the three species for which reproductive anatomy is known.

Etymology. This name honors Dr. Carl C. Christensen for the many years he devoted to studying highly endangered terrestrial snails from the Pacific Islands, especially the Hawaiian Islands, and recognition of his efforts to bring attention to the status of this undescribed species.

DISCUSSION

The land snails of Nihoa represent one of the last vestiges of the fauna that once inhabited lower elevation habitats across the Hawaiian Islands (Conant *et al.* 1984). Pacific island land snails are particularly sensitive to ecological degradation (Paulay 1994, Keppel *et al*. 2014, Chiba & Cowie 2016) and like the proverbial "canary in the coal mine", their extinctions herald environmental changes that can impact other biota. However, little is known regarding the population dynamics of minute snails on remote islands (Gargominy *et al.* 2020) and attention to terrestrial gastropods in the Northwestern Hawaiian Islands has been intermittent at best. As a result, population declines of these species are likely to go unnoticed.

Nihoa's small size, approximately 1.5 km × 0.5 km, makes its fragile biota extremely vulnerable to habitat loss. For example, in 1885, visitors to the island accidentally ignited a wildfire that burned almost 2/3 of the island (Rauzon 2001, Evenhuis & Eldredge 2004). Land snail surveys by Thaanum and Cooke in 1923 found that *Endodonta christenseni* sp. nov. was locally abundant in bunch grasses except in the two central valleys of the island where the fire had raged (Cooke in litt. 1923). Although the palms seem to rebound quickly from these fires (Evenhuis & Eldredge 2004), Cooke (*in litt*. 1923) noted the snail fauna had not fully recolonized these areas even 40 years after the fire. Surveys conducted in 2015 found these areas still devoid of snails despite the presence of appropriate plants. Introduced species can also have devastating impacts on habitats on such a small island (Evenhuis & Eldridge 2004). In the early 2000s the invasive gray bird grasshopper (*Schistocerca nitens*) reached high abundances several times following drought conditions. During these events grasshoppers denuded much of the vegetation and continue to negatively impact once abundant plant species on the island, such as *Chenopodium oahuense* and *Sesbania tomentosa* (Latchininsky 2008).

Aside from being found in *Eragrostis variabilis* little is known about what other plants or ecosystem resources that these snails rely on for survival. It is possible that drought conditions in combination with the denudation of vegetation, and the reduction in abundance of once common plants, have already negatively impacted snail populations. It is also likely that global warming and associated increases in droughts may exacerbate both fire danger and impacts of non-native species on native flora (Evenhuis & Eldridge 2004, Mainka & Howard 2010).

Despite being extremely isolated and currently uninhabited, Nihoa has not entirely escaped the introduction of snail predators, which have devastated snail populations throughout the Pacific. Evenhuis & Eldridge (2004) list nine species of ants on Nihoa, but in their surveys Plentovich *et al.* (2013) collected only four ant species. It is likely that ant infestations began in low elevation areas where anthropogenic activity is highest. Interestingly, during the most recent surveys in 2015, no snails were found in sites below 96 m elevation, even if the habitat seemed suitable. While this is anecdotal at best, it should be noted that areas with detectable ants lacked snails, a pattern often seen in the main Hawaiian Islands. While often implicated in snail extinctions (Solem 1976), limited research has been conducted looking at the negative impacts of ants on snail species (Uchida *et al.* 2016). However, it is likely that ants adversely impact minute snails as they do other invertebrate species (Howarth 1985, LaPolla *et al*. 2000, Wetterer 2007), through direct predation and or habitat alteration.

Despite 15 years of sampling across more than 1000 sites throughout the Hawaiian archipelago, none of the 11 previously described species of *Endodonta* has been observed in our studies and it is likely that all are extinct. *Endodonta christenseni* sp. nov. is the only known extant member of the genus and quite possibly the last. Unless there are conservation strategies in place to protect this species, an entire genus faces extinction. This would represent the irreversible loss of an entire lineage and with it, millions of years of evolutionary history, which continues to inform a broader understanding of biodiversity in the islands.

Recently, *Cookeconcha hystricella*, the closest extant relative of *E. christenseni* sp. nov., has been successfully reared for multiple generations in captivity and has been reintroduced into the wild on the island of Oahu. It is likely that *E. christenseni* sp. nov. would fare equally well under captive conditions. If successful, captive-reared individuals could be released on Nihoa to augment existing populations and repopulate areas where the species was extirpated during historical fire events. Captive-reared individuals could also be used to expand its range to other restored Northwestern Hawaiian Islands, or even in restored areas within the higher main Hawaiian Islands, that have lost their endemic species.

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