Overlooked but not forgotten: the first new extant species of Hawaiian land snail described in 60 years, *Auriculella gagneorum* sp. nov. (Achatinellidae, Auriculellinae)

Norine W. Yeung¹, John Slapcinsky², Ellen E. Strong³, Jaynee R. Kim¹, Kenneth A. Hayes¹

¹ Bishop Museum, 1525 Bernice Street, 96817, Honolulu, Hawaii ² Florida Museum of Natural History, 1659 Museum Road, 32611, Gainesville, Florida ³ National Museum of Natural History, Smithsonian Institution, PO Box 37012, MRC 163, 20013-7012, Washington, DC, USA

Corresponding author: Norine W. Yeung (nyeung@hawaii.edu)

Abstract

Recent surveys of Oahu's Waianae Mountains uncovered a small, previously undescribed species of *Auriculella* that is conchologically similar to the three members of the *A. perpusilla* group all of which are endemic to the Koolau Mountain Range. However, sequence data demonstrate that the *perpusilla* group is not monophyletic. Moreover, the new species is not closely related to *A. perpusilla* or *A. perversa*, the only extant members of the group, but instead is sister to *A. tenella*, a species from the high spired *A. castanea* group. A neotype is designated for *A. auricula*, the type species of *Auriculella*; all members of the conchologically similar *perpusilla* group are anatomically redescribed; and lectotypes designated for *A. minuta*, *A. perversa*, and *A. tenella*. The new species is described and compared to the type of the genus, members of the *perpusilla* group, and the genetically similar species *A. tenella*.

Keywords
gastropod, island, Oahu, Pacific, systematics
Introduction

Pacific Island land snails are among the most threatened faunas in the world, with more recorded extinctions since 1600 than any other group of animals (Régnier et al. 2009). Of the more than 25,000 islands spread across the Pacific, few have been extensively surveyed in modern times for their invertebrate fauna, and the estimates of extinction are probably a vast underestimate. Of the few islands and archipelagos that have been studied, like Hawaii, extinctions have been shown to be extensive (Régnier et al. 2015; Yeung and Hayes 2018). For example, as much as 93% of the endemic family Amastridae has been lost, and the other 12 families of land snails represented in Hawaii are not faring much better (Yeung and Hayes 2018). Critical to understanding and slowing the rate of extinction is accurate and updated systematics and biogeography of land snails, and other understudied groups (Cardoso et al. 2011).

The Pacific Island family Achatinellidae is the second most diverse land snail family in the Hawaiian Islands with 209 species divided into five subfamilies, two of which, the Achatinellinae Gulick, 1873 and Auriculellinae Odhner, 1922, are endemic (Cooke and Kondo 1960). Historically the large and colorful Achatinellinae have garnered much attention and the lion’s share of molluscan conservation attention in Hawaii (Gulick 1872; Hadfield et al. 1993; Thacker and Hadfield 2000; Holland and Hadfield 2002, 2004, 2007; Erickson and Hadfield 2008; Hadfield and Sauffer 2009; O’Rorke et al. 2015; Price et al. 2015, 2016a, b, 2018; Sischo et al. 2016), and include the only Hawaiian land snail species protected under the US Endangered Species Act (1981, 2013). However, the smaller, less colorful Auriculellinae, comprising 31 species in the genus Auriculella Pfeiffer, 1854 and one species in the genus Gulickia Cooke in Pilsbry & Cooke, 1915 have remained understudied and unprotected since the last revisions more than a century ago (Pilsbry and Cooke 1914–1916). Although fossils (Solem 1977; Severns 2009) and extinct species (Severns 2011) of Hawaiian land snails have continued to be described, no new extant species of native Hawaiian land snails have been described in more than 60 years. The last described extant Hawaiian land snail species was an achatinellid in the subfamily Tornatellidinae Cooke & Kondo, 1960, Philopoa singularis Cooke & Kondo, 1960 and the most recently described Auriculella species is A. lanaiensis Cooke in Pilsbry & Cooke, 1915.

Cooke and Kondo (1960) arranged Auriculella into four conchologically distinct groups: the cerea group from the southeastern islands of Hawaii, Lanai, Maui, and Molokai; and the auricula, castanea, and perpusilla groups which are all endemic to Oahu (Pilsbry and Cooke 1914–1916; Cooke and Kondo 1960). The perpusilla group (A. perpusilla Smith, 1873, A. minuta Cooke & Pilsbry in Pilsbry & Cooke, 1915, and A. perversa Cooke in Pilsbry & Cooke, 1915) contains the smallest species; all 6 mm or less in adult shell height. In addition to their small size these species have thin shells with 5 strongly convex whorls with low spires and weakly reflected apertures distinguishing them from the many-whorled, high-spired castanea group and the larger, thicker shelled auricula and cerea groups (Pilsbry and Cooke 1914–1916).

In addition to their morphological similarity, the three species in the perpusilla group are all endemic to Oahu’s eastern Koolau range (Fig. 1B–D). Recent collecting
The first new species of Hawaiian land snail described in 60 years

Auriculella auricula B Auriculella minuta C Auriculella perpusilla D Auriculella perversa E Auriculella tenella and F Auriculella gagneorum sp. nov. Dark grey circle = historical; light grey triangle = since 2010.

in the island’s western Waianae range uncovered a previously undescribed species with features of shell size and shape that would place it in this group. The two mountain ranges are separated by a relatively dry, low elevation saddle 22 km long and 8 km wide and few land snail species have distributions in both ranges (Pilsbry and Cooke 1914–1916; Cowie et al. 1995). Specimens of the undescribed species were also found in samples collected prior to 1940, which were housed in the Bishop Museum (BPBM) and labelled by Y. Kondo as a potentially new species.
Within *Auriculella*, intraspecific shell morphology varies and may often overlap interspecifically, making species delineation based on conchology alone difficult (Pilsbry and Cooke 1914–1916). As such, additional morphological and molecular data (e.g., DNA and RNA sequences) are necessary to distinguish among closely related species. The reproductive anatomy of only a few *Auriculella* species is known. Pilsbry and Cooke (1915 on plate 22) figured *A. pulchra* Pease, 1868 (figs 1, 2); *A. cerea* (Pfeiffer, 1855) (fig. 3); and *A. armata* (Mighels, 1845) as *A. westerlundiana* Ancey, 1889 (fig. 6). The reproductive anatomy of the type species of the genus, *Auriculella auricula* (Férussac, 1821), was figured and described by Cooke and Kondo (1960: figs 113a–d, 114a–c) who also dissected 22 other species but figured only *A. castanea* (Pfeiffer, 1853) (Cooke and Kondo 1960: fig. 114d). The reproductive anatomy of the other species has never been figured or described, including all members of the *perpusilla* group. As part of a broader project whose aim is to fully revise the systematics of the Achatinellidae, we use an integrative approach using data from conchology, radula, reproductive system, and DNA sequences, to redescribe *A. auricula*, the type species of the genus and all members of the *perpusilla* group (*A. perpusilla*, *A. minuta*, and *A. perversa*). We also describe a new species, *A. gagneorum* sp. nov., based on recently collected material and from lots housed in the Bishop Museum. Relationships of the taxa traditionally relegated to the *perpusilla* group, and of the conchologically similar *A. gagneorum* sp. nov., are explored with a mitochondrial and nuclear gene dataset. To enhance the stability of the nomenclature, we designate a neotype for *A. auricula* and lectotypes for members of the *perpusilla* group.

**Materials and methods**

As part of a long-term study of extant Hawaiian land snails, our team has surveyed more than 1000 sites across the six largest Hawaiian Islands (Kauai, Oahu, Maui, Molokai, Lanai, Hawaii). The targeted locations were those that historically supported snail populations, as well as more remote areas with remnant native vegetation that were often accessible only by helicopter. Surveys followed Durkan et al. (2013) and consisted of leaf litter sampling and hand collecting for at least one-person-hour by a minimum of two experienced malacologists in quadrats of at least 10 m², but up to 100 m², terrain permitting. GPS coordinates were collected at every survey site and coordinates were estimated for historical BPBM specimen records using locality, field notes, maps, and other descriptions. The precise locations (e.g., GPS coordinates) for material listed are not provided here for conservation purposes but are kept in the State of Hawaii Department of Land and Natural Resources Snail Extinction Prevention Program and Bishop Museum Malacology databases. Distributional maps were created using QGIS v3.8.2 (QGIS 2019) and used to show historical and current distributions of the species treated herein.

Newly collected material was photographed, flash boiled (Fukuda et al. 2008), and then fixed in 95% ethanol, after which a small piece of foot tissue was removed for DNA extraction. The remaining soft tissues were preserved in 80% ethanol, and dissections
were performed on preserved specimens submerged in 75% ethanol. Shells and reproductive anatomy were photographed with digital single-lens reflex cameras (e.g., Cannon EOS 7D) attached to a dissecting microscope. Photographs of reproductive anatomy were traced in Photoshop to produce line drawings. Shell measurements were made using an ocular micrometer and each measurement was repeated three times and averaged for 50 specimens per species. Shell measurements, shell height (H), shell width (W), aperture height (AH), aperture width (AW), and number of whorls (WH) were made following Slapcinsky and Kraus (2016: 30, fig. 1). All pertinent type and comparative material were examined and photographed. Locality and collector information of materials examined were listed as verbatim. Materials examined for the new species is provided in the text and all others can be found in Suppl. material 1. Museum collections are abbreviated:

ANSP Academy of Natural Sciences, Philadelphia;
BPBM Bernice P. Bishop Museum, Honolulu;
MCZ Museum of Comparative Zoology, Cambridge;
MNHN Muséum national d’Histoire naturelle, Paris;
NMW National Museum of Wales, Cardiff;
RBINS Royal Belgian Institute of Natural Sciences, Brussels;
SMF Naturmuseum Senckenberg, Frankfurt.

Radulae were tissue-digested in 180 µL of T1 lysis buffer (Macherey-Nagel) containing 20 mg/mL of Proteinase-K and rinsed in de-ionized water. Cleaned radulae were 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 an Apreo scanning electron microscope (FEI Company) at the National Museum of Natural History, Washington.

Total genomic DNA (gDNA) was extracted from an approximately 1 mm³ piece of foot tissue using the 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, and gDNA stored at -20 °C prior to amplification via the polymerase chain reaction (PCR).

Portions of two mitochondrial genes, 16S ribosomal DNA (rDNA) and cytochrome c oxidase subunit I (COI), and the nuclear encoded 28S rDNA were amplified using primers listed in Table 1. 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 MgCl₂ and 0.75 µM of each primer, 10 µg BSA, and 0.5% DMSO. Cycling parameters were one cycle of 5 min at 95 °C, 1 min at 44–48 °C, 2 min at 72 °C, followed by 34 cycles of 95 °C, 46–50 °C,

| Locus | T°C | Primers F/R |
|-------|-----|-------------|
| COI   | 44-46 | LCO1490/HCO2198 (Folmer et al. 1994) |
| 16S   | 48-50 | 16Sar/16S2 (Palumbi 1996; Garey et al. 1998) |
| 28S   | 46-48 | LSU2/LSU5 (Wade et al. 2006) |
and 72 °C for 30 sec each, and a final extension of 5 min at 72 °C. A final 4 °C incubation of 30 min terminated each reaction (Table 1). The amount and specificity of amplifications were verified via agarose electrophoresis and single product amplicons were cycle sequenced using the ABI BigDye terminator kits (Perkin-Elmer Applied Biosystems, Inc.). Sequences were electrophoresed and analyzed on an ABI 3730XL (Perkin-Elmer Applied Biosystems, Inc.) at either the University of Hawai‘i’s Advanced Studies in Genomics, Proteomics, and Bioinformatics facility or Eurofins Genomics, LLC. All loci were initially sequenced in one direction, and any unique haplotypes sequenced in both directions. The COI fragment was sequenced for all individuals, and subsets of these were selected based on unique COI haplotypes and sequenced for 16S and 28S. Due to lower variability in the other two loci, not all individuals with a unique COI haplotype were sequenced for all other loci. All sequences have been uploaded to the Barcode of Life Data System (BoLD; https://doi.org/10.5883/DS-AURICOI) and to GenBank (Accession numbers MT519807–MT519913; Table 2)

Electropherograms were checked for errors, edited, and assembled using Geneious Prime 2019 (http://www.geneious.com/). Sequences of COI were unambiguously aligned using MAFFT ver. 7.388 with the iterative refinement method E-INS-I (Katoh and Standley 2013) implemented in Geneious Prime 2019. Alignments where checked against amino acid sequences as references. Ribosomal genes were aligned using MAFFT and refined using Gblocks ver. 0.91b (Castresana 2000). Refinement of the 16S and 28S alignments in Gblocks removed regions of ambiguous homology created by the addition of gaps during initial alignment and the hypervariable nature of some regions. Phylogenetic analyses were done with and without these regions to evaluate their impact. Sequence alignments were concatenated in Geneious Prime and 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 5,000 ultra-fast bootstrap replicates (Hoang et al. 2018).

To corroborate species delineation based on conchological and anatomical analyses and phylogenetic reconstruction, we used the DNA barcode-based species identification method implemented in SpeciesIdentifier ver. 1.8 (Meier et al. 2006).

Museum catalog numbers for specimens used in DNA analysis with numbers of specimens from which shell measurements, reproductive anatomy, and radular morphology were obtained, are listed in Table 2.

Results

Recent surveys recorded extant populations of two of the three species within the perpusilla group: A. perpusilla and A. perversa (Fig. 1C, D, respectively) and a new spe-
The first new species of Hawaiian land snail described in 60 years

**Table 2.** Museum catalog numbers for specimens used in genetic analysis with numbers of specimens from which shell measurements, reproductive anatomy and radular morphology were obtained. Catalog numbers (BPBM) are for lots from which specimens were sequenced (N = number of individuals sequenced from each lot).

| Genus    | Species | Island | BPBM          | COI            | 16S            | 28S            | Shell measurements | Reproductive system | Radula |
|----------|---------|--------|---------------|----------------|----------------|------------------|-------------------|---------------------|--------|
| Auriculella | ambusta | Oahu   | BPBM 285779 (1) | MT519807 | –             | MT519879       | –                 | –                   | –      |
|          |         | Oahu   | BPBM 285779 (1) | MT519813 | MT519861     | MT519880       | –                 | –                   | –      |
|          |         | Oahu   | BPBM 285780 (1) | MT519808 | MT519860     | –               | –                 | –                   | –      |
|          |         | Oahu   | BPBM 285781 (1) | MT519809 | –             | –               | –                 | –                   | –      |
|          |         | Oahu   | BPBM 285782 (2) | MT519810 | –             | –               | –                 | –                   | –      |

| Genus | Species | Island | BPBM          | COI            | 16S            | 28S            | Shell measurements | Reproductive system | Radula |
|-------|---------|--------|---------------|----------------|----------------|------------------|-------------------|---------------------|--------|
|       | aura    | Oahu   | BPBM 119141   | –              | –              | –               | –                 | –                   | –      |
|       |         | Oahu   | BPBM 119157   | –              | –              | –               | –                 | –                   | –      |
|       |         | Oahu   | BPBM 119172   | –              | –              | –               | –                 | –                   | –      |
|       |         | Oahu   | BPBM 12651    | –              | –              | –               | –                 | 1                   | –      |
|       |         | Oahu   | BPBM 12666    | –              | –              | –               | –                 | 21                  | –      |
|       |         | Oahu   | BPBM 164138   | –              | –              | –               | –                 | –                   | 1      |
|       |         | Oahu   | BPBM 189709   | –              | –              | –               | –                 | –                   | –      |
|       |         | Oahu   | BPBM 189710   | –              | –              | –               | –                 | –                   | –      |
|       |         | Oahu   | BPBM 190854   | –              | –              | –               | –                 | –                   | –      |
|       |         | Oahu   | BPBM 285783   | –              | –              | –               | –                 | –                   | –      |

|       | auricula | Oahu  | BPBM 119141   | –              | –              | –               | –                 | –                   | –      |
|       |          | Oahu  | BPBM 119157   | –              | –              | –               | –                 | –                   | –      |
|       |          | Oahu  | BPBM 119172   | –              | –              | –               | –                 | –                   | –      |
|       |          | Oahu  | BPBM 12651    | –              | –              | –               | –                 | 1                   | –      |
|       |          | Oahu  | BPBM 12666    | –              | –              | –               | –                 | 26                  | –      |
|       |          | Oahu  | BPBM 164138   | –              | –              | –               | –                 | –                   | –      |
|       |          | Oahu  | BPBM 189709   | –              | –              | –               | –                 | –                   | 1      |
|       |          | Oahu  | BPBM 189710   | –              | –              | –               | –                 | –                   | –      |
|       |          | Oahu  | BPBM 190854   | –              | –              | –               | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285783   | –              | –              | –               | –                 | –                   | –      |

|       | auricula | Oahu  | BPBM 285784 (1) | MT519819 | –              | MT519888       | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285785 (1) | MT519813 | MT519863     | MT519888       | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285786 (1) | MT519813 | MT519863     | MT519888       | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285787 (3) | BPBM 285793 (3) | MT519816 | MT519863       | MT519885 | –                 | –      |
|       |          | Oahu  | BPBM 285791 (5) | BPBM 285792 (1) |              |              |              | –                 | –      |
|       |          | Maui  | BPBM 285788 (1) | MT519815 | MT519864     | MT519884       | –                 | –                   | –      |
|       |          | Maui  | BPBM 285788 (2) | MT519813 | MT519863     | MT519888       | –                 | –                   | –      |
|       |          | Maui  | BPBM 285789 (4) | BPBM 285788 (2) | MT519813 | MT519863     | MT519888       | –                 | –      |
|       |          | Maui  | BPBM 285790 (3) | BPBM 285791 (5) | MT519816 | MT519863       | MT519885 | –                 | –      |
|       | gagneorum sp. nov, | Oahu  | BPBM 174233 | –              | –              | –               | –                 | 7                   | –      |
|       |          | Oahu  | BPBM 21823    | –              | –              | 40              | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285794 (1) | BPBM 285844 (1) | BPBM 285796 (1) | MT519823 | MT519891 | –                 | –      |
|       |          | Oahu  | BPBM 285795 (1) | BPBM 285796 (1) | MT519826 | –              | –               | –                   | –      |
|       |          | Oahu  | BPBM 285796 (1) | BPBM 285794 (1) | MT519820 | MT519866     | MT519889       | –                 | –      |
|       |          | Oahu  | BPBM 285797 (1) | BPBM 285797 (1) | MT519821 | MT519867     | MT519890       | –                 | 1      |
|       |          | Oahu  | BPBM 285797 (1) | BPBM 285798 (1) | MT519824 | MT519892     | –               | –                   | –      |
|       |          | Oahu  | BPBM 285798 (1) | BPBM 285799 (1) | BPBM 285800 (2) | BPBM 285843 (1) | MT519822 | MT519868 | –                 | – |
|       | malleata | Oahu  | BPBM 285801 (1) | MT519830 | –              | MT519894       | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285801 (1) | MT519831 | –              | MT519895       | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285802 (1) | MT519829 | MT519869     | MT519893       | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285803 (3) | MT519828 | –              | –               | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285804 (1) | MT519832 | MT519870     | MT519896       | –                 | –                   | –      |
|       |          | Oahu  | BPBM 285804 (1) | MT519827 | –              | –               | –                 | –                   | –      |

|       | minuta | Oahu  | BPBM 12799    | –              | –              | –               | –                 | 14                  | –      |
|       |         | Oahu  | BPBM 12804    | –              | –              | –               | –                 | 25                  | –      |
|       |         | Oahu  | BPBM 170304   | –              | –              | –               | –                 | 10                  | –      |
|       |         | Oahu  | BPBM 98043    | –              | –              | –               | –                 | –                   | –      |
|       |         | Oahu  | BPBM 993164   | –              | –              | –               | –                 | –                   | 2      |
| Genus     | Species   | Island | BPBM       | COI         | 16S         | 28S         | Shell measurements | Reproductive system | Radula |
|-----------|-----------|--------|------------|-------------|-------------|-------------|-------------------|---------------------|--------|
| *Auriculella* | *minuta* | Oahu   | BPBM 99164 | –           | –           | –           | –                 | –                   | 3      |
|           | *montana* | Oahu   | BPBM 285805 (1) | MT519833     | –           | –           | –                 | –                   | –      |
|           | *perpusilla* | Oahu   | BPBM 122645 | –           | –           | 15          | –                 | –                   | –      |
|           |           | Oahu   | BPBM 134280 | –           | –           | 15          | –                 | –                   | –      |
|           |           | Oahu   | BPBM 134451 | –           | –           | 15          | –                 | –                   | –      |
|           |           | Oahu   | BPBM 15048  | –           | –           | 4           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285806 (1) | MT519837     | –           | –           | –                 | –                   | 1      |
|           |           | Oahu   | BPBM 285807 (1) | MT519835     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285808 (1) | MT519836     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 90853  | –           | –           | –           | 2                 | –                   | –      |
|           |           | Oahu   | BPBM 93626  | –           | –           | –           | 5                 | 2                   | –      |
| *perversa* |           | Oahu   | BPBM 12798  | –           | –           | 15          | –                 | –                   | –      |
|           |           | Oahu   | BPBM 164180 | –           | –           | –           | –                 | 2                   | –      |
|           |           | Oahu   | BPBM 22767  | –           | –           | 34          | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285809 (1) | MT519839     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285810 (2) | MT519838     | –           | –           | 1                 | 2                   | –      |
|           |           | Oahu   | BPBM 97904  | –           | –           | –           | 1                 | –                   | 2      |
|           | *tenella* | Oahu   | BPBM 125606 | –           | –           | 7           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 162927 | –           | –           | –           | 1                 | –                   | –      |
|           |           | Oahu   | BPBM 18943  | –           | –           | –           | 1                 | –                   | –      |
|           |           | Oahu   | BPBM 211034 | –           | –           | –           | 1                 | –                   | –      |
|           |           | Oahu   | BPBM 285811 | –           | –           | –           | 2                 | –                   | –      |
|           | *torriella* | Oahu   | BPBM 285812 (1) | MT519841     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285812 (1) | MT519842     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285813 (1) | MT519843     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285814 (1) | MT519844     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285815 (1) | MT519845     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285816 (1) | MT519846     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285817 (1) | MT519847     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 33194  | –           | –           | –           | 42                | –                   | –      |
|           | *turritella* | Oahu   | BPBM 285818 (1) | MT519848     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285819 (1) | MT519849     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285820 (1) | MT519850     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285821 (1) | MT519851     | –           | –           | 3                 | –                   | –      |
|           |           | Oahu   | BPBM 285823 (1) | MT519852     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285824 (1) | MT519853     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285830 (1) | MT519854     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285831 (1) | MT519855     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285832 (1) | MT519856     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285833 (1) | MT519857     | –           | –           | –                 | –                   | –      |
|           |           | Oahu   | BPBM 285834 (1) | MT519858     | –           | –           | –                 | –                   | –      |
|           | *uniplicata* | Maui   | BPBM 285836 (1) | MT519859     | –           | –           | –                 | –                   | –      |
|           |           | Maui   | BPBM 285836 (1) | MT519860     | –           | –           | –                 | –                   | –      |
|           |           | Maui   | BPBM 285837 (1) | MT519861     | –           | –           | –                 | –                   | –      |
|           |           | Maui   | BPBM 285838 (1) | MT519862     | –           | –           | –                 | –                   | –      |
|           |           | Maui   | BPBM 285839 (1) | MT519863     | –           | –           | –                 | –                   | –      |
|           |           | Maui   | BPBM 285840 (1) | MT519864     | –           | –           | –                 | –                   | –      |
| *Tornatellaria* | *sp.*  | Maui   | BPBM 285841 (1) | MT519865     | –           | –           | –                 | –                   | –      |
|           |           | Maui   | BPBM 285842 (1) | MT519866     | –           | –           | –                 | –                   | –      |
|           | *Tornatellides* | Molokai | BPBM 285843 (1) | MT519867     | –           | –           | –                 | –                   | –      |
The first new species of Hawaiian land snail described in 60 years (A. gagneorum) was described with similar shell morphology, A. auricula (type species of the genus), and A. minuta. No populations of A. auricula (type species of the genus) or A. minuta were recorded in our surveys and both species may be extinct.

The 104 snails representing ten Auriculella species and two outgroup taxa (Tornatellaria sp. and Tornatellides sp.) sequenced for this study produced 53 COI haplotypes, 19 and 35 sequences for 16S and 28S, respectively. Alignments for each locus were 654 bp for COI, 464 bp for 16S and 539 bp for 28S, making the concatenated dataset of 53 individuals 1657 bp with 223 parsimony informative sites. Sixteen individuals were represented by all three loci, while three individuals had only COI and 16S, 19 with COI and 28S, and 15 with only COI. The best-fit partitioning scheme used distinct models for each locus with the best-fit models being K3Pu+F+I+G4, TPM2u+F+G4, and TIM3+F for COI, 16S, and 28S respectively.

The ML tree constructed from the concatenated dataset produced a well-resolved tree with all conchologically defined taxa recovered in strongly supported clades (Fig. 2). None of the groupings suggested by Cooke and Kondo (1960) based on gross shell morphology were recovered in the ML tree. As such, A. perpusilla and A. perversa, previously referred to the perpusilla group were recovered in unrelated clades with each as sister to much larger shelled species, A. ambusta and A. montana, respectively. Similarly, the new species Auriculella gagneorum was recovered as sister to A. tenella and not close to A. perpusilla or A. perversa, with which it was previously confused.

The best match/best close match criteria (Meier et al. 2006) applied to all 53 COI haplotypes successfully matched all sequences in the correct conspecific clusters within a 3–4% threshold consistent with conchologically and phylogenetically recognized clades. Correct identifications with both approaches was 94.33%, with the other 5.66% (three sequences) lacking any conspecific sequences with which to cluster. These included the two outgroup taxa and A. montana, all of which were represented by a single sequence.

Systematics

Class Gastropoda Cuvier, 1795
Subclass Heterobranchia Burmeister, 1837
Order Stylommatophora A. Schmidt, 1855
Superfamily Pupilloidea W. Turton, 1831
Family Achatinellidae Gulick, 1873
Subfamily Auriculellinae Odhner, 1921

Genus Auriculella Pfeiffer, 1854

Type species. Partula auricula Férussac, 1821 by subsequent designation (Gulick 1873).

Diagnosis. Small to moderately sized Achatinellidae, 4 to 12 mm in adult shell height. Shells either dextral or sinistral, taller than wide, with a strong parietal la-
Figure 2. Phylogenetic tree of ten *Auriculella* spp. produced via Maximum Likelihood using a concatenated matrix composed of partial sequences of COI, 16S and 28S. Shapes on the nodes correspond to ML bootstrap values of 70–79 (triangle), 80–89 (circle), and 90–100 (square).

Juvenile shells have two columellar lamellae, one or both of which are lacking in adults. Phallus with an epiphallus and a nearly apical appendix. Phallus retractor muscle inserted apically on the epiphallus and not secondarily attached to the appendix. Members of *Auriculella* are the only achatinellids known to have an epiphallus. All *Auriculella* species are oviparous (Pilsbry and Cooke 1914–1916).
The first new species of Hawaiian land snail described in 60 years

*Auriculella auricula* (Férussac, 1821)
Figures 1A, 3A, B, 4A, 5A

*Partula auricula* Férussac, 1821: 66.

*Auriculella auricula* – Gulick 1872: 222; Gulick 1873: 91; Pilsbry and Cooke 1915: 78–80, pl. 24, figs 1–10; Cooke and Kondo 1960: 270–272, figs 113a–e, 114a–c; Cowie et al. 1995: 75; Severns 2011: 206, pl. 80, fig. 2.

**Type material. Neotype:** USA • 1; H = 8.7 mm, W = 4.2 mm, AH = 4.6 mm, AW = 3.3 mm, with 6.4 WH; Honolulu County, Oahu, Koolau Mountains, Tantalus; 09 Jun 1943; Y. Tanada leg.; BPBM 189709.

**Type locality.** “Sans doute les îles de la mer du Sud?” [without doubt the south sea islands?]; colloquially “sans doute” means probably; here restricted to Tantalus.

**Diagnosis. Shell.** Shell dextral or sinistral with flat-sided whorls and an obtuse apex, H = 8.0 ± 0.4 mm, W = 4.3 ± 0.2 mm, WH 6.0 ± 0.2, AH = 4.1 ± 0.2 mm, AW = 3.1 ± 0.2 mm (N = 50; Table 2). Columella with a single strong lamella and without an axial ridge. Parietal lamella is strong and smooth and not undulate, extending 0.3 to 0.7 whorls into the aperture. Shell color is tan, brown, or yellowish, often with a single narrow brown or white band (Fig. 3B). White bands are sometimes bordered by two darker brown bands and apical whors are often darker brown. Lip reflected, thickened, white or brown in color.

**Reproductive system.** Phallus retractor muscle relatively long, attached apically to a short but well-defined epiphallus (Fig. 4A). Appendix is longer than the phallus and about ⅗ the diameter of the phallus at its attachment. The appendix narrows abruptly at ⅘ its length and remains narrow to its terminus. Phallus is broad, narrowing only slightly apically and basally. Atrium is relatively short and broad. Vagina is about ⅓ the length of the phallus.

**Radula.** Radula with an irregular rachidian flanked on either side by rastriform marginal teeth, as diagnostic of the family (Fig. 5A). Each tooth has a long narrow base that expands slowly for ⅗ of the length of the tooth before reaching the forward curving cusps, which comprise the remaining ¼ of the tooth. There are three long cusps at mesocone, endocone, and ectocone positions with two or more alternating larger and smaller cusps intercalated between them. Number of teeth per row range from 177 to 183 (N = 6; Table 2).

**Distribution and ecology.** *Auriculella auricula* is endemic to Oahu’s Koolau Mountains (Fig. 1A), historically found across the range at elevations from 61 m to 305 m. The species is arboreal and found on vegetation including: *Cordyline* sp. *Frey-cinetia arborea*, *Metrosideros polymorpha*, *Canna* sp. (BPBM 34025, 49056, 51405), *Aleurites moluccanus*, *Psychotria* sp., *Zingiber* sp., *Psidium cattleyanum*, *Musa* sp., *As-pleniun* sp., and unspecified ferns and shrubs. The species has also been recorded on the ground under stones, logs and dead leaves. Live specimens recorded in the BPBM collection were last collected by Y. Kondo in 1946 from Palolo Valley; the species has not been recorded in recent surveys and is considered here possibly extinct.
Figure 3. Comparative shell morphology of **A** *Auriculella auricula* neotype BPBM 18709 **B** *Auriculella auricula* shell variation (left to right) BPBM 12651, BPBM 12666 **C** *Auriculella minuta* lectotype BPBM 42377 **D** *Auriculella minuta* shell variation (left to right) BPBM 12804, paralectotype MCZ 73037 **E** *Auriculella perpusilla* holotype MCZ 39912 **F** *Auriculella perpusilla* (left to right) BPBM 285806, BPBM 134341 (2 spm), BPBM 134280 white one, BPBM 122643, BPBM 13443 **G** *Auriculella perversa* lectotype BPBM 42384, 3 shells **H** *Auriculella perversa* shell variation (left to right) paralectotype ANSP 91817 **I** *Auriculella tenella* lectotype BPBM 18943 **J** *Auriculella tenella* shell variation paralectotype BPBM 109679 **K** *Auriculella gagneorum* sp. nov. holotype (BPBM 285843) and **L** *Auriculella gagneorum* sp. nov. paratypes, left to right (BPBM 285797, 285794, 285795, 285798). Scale bar: 5 mm.
Remarks. In the original description, Férussac (1821) provided measurements for a single shell of three lines (6.8 mm) in height and 1¾ lines (4.0 mm) in width. His collection is housed in MNHN where there are two lots labelled *A. auricula* that are attributed to Férussac. The first (MNHN IM-2000-34306, 34307, 34308) is from Férussac’s collection but does not contain original labels. The three dextral shells are identified as *A. auricula* from the Mariana Islands, but they are not *A. auricula* and instead appear to be a gerontic adult and two juveniles similar to *Auriculella ambusta*, a species not found on the same mountain range as *A. auricula*. The other lot (MNHN IM-2014-7009) is from the Deshayes collection. Its source is unknown but probably came from Férussac whose specimens Deshayes used to complete Férussac’s “Histoire naturelle des mollusques terrestres et fluviales” after Férussac’s death in 1836. The lot contains six specimens of *Auriculella pulchra*, two of which are sinistral and all of which are larger than 6.8 mm. The two lots are not consistent with Férussac’s description, and we exclude these lots as possible syntypes of *A. auricula*. We have not located any other type material of *A. auricula* and we consider the types to be lost. Stabilizing the nomenclature of this species is important because it is the type species of the genus *Auriculella*, a genus with many similar but conchologically variable and poorly resolved species, nearly all of which are highly endangered. We designate BPBM 18709 (Fig. 3A) from Tantalus, Oahu as neotype of *Auriculella auricula* to stabilize the taxonomic status and type locality of the species as well as the genus *Auriculella*. The neotype matches Férussac’s original description in having an acute ovoid shell with an obtuse apex, strong parietal lamella, and single columellar lamella. The color of the neotype is more tan than yellowish as described in the original description but the species is known to be polymorphic for shell color and pattern as well as chirality. The shell used in Férussac’s description was sinistral while the neotype is dextral. We chose a dextral specimen with slightly different coloration because it was used by Cooke and Kondo (1961) to describe the nervous system and reproductive anatomy of *Auriculella auricula* thus clearly defining the species as well as the genus. The other four specimens from BPBM 189709 are re-cataloged as BPBM 285783. One of these is a broken shell presumably corresponding to the animal dissected by Cooke and Kondo (1961).

*Auriculella minuta* Cooke & Pilsbry, 1915

Figures 1B, 3C, D, 4B, 5B

*Auriculella minuta* Cooke & Pilsbry in Pilsbry & Cooke, 1915: 90, pl. 25, figs 5–9; Cowie et al. 1995: 76; Johnson 1996: 190; Severns 2011: 210, pl. 82, fig. 1.

Type material. **Lectotype:** USA • 1, H = 4.9 mm, W = 2.8 mm, AH = 2.2 mm, AW = 1.7 mm, WH = 5.7.; Honolulu County, Oahu, Koolau Mountains, Nuuanu; Nuuanu Valley Ridge 7, east, on ti, lehua, *Passiflora foetida*; Cooke leg.; BPBM 42377, here designated

**Paralectotypes:** USA – Honolulu County, Oahu, Koolau Mountains • 1; Nuuanu Valley; Cooke leg.; BPBM 42377 • 1; Nuuanu Ridge; BPBM 13034 • 2; Nuuanu;
BPBM 42379 • 1; Nuuanu Ridge; Cooke leg.; BPBM 42380 • 33; Nuuanu Ridge; Cooke leg.; BPBM 4238 • 1; Nuuanu Valley; Cooke leg.; BPBM 42382 • 82; Nuuanu Valley; Cooke leg.; BPBM 42383 • 5, Palolo Valley; Lyman leg.; BPBM 12808

Paralectotypes not examined. ANSP 91816 (11 spm), ANSP 113294 (10 spm), MCZ 73037 (5 spm), SMF 7127 (4 spm), BPBM 12808 (5 spm).

Possible paralectotype. USA – Honolulu County, Oahu, Koolau Mountains • 6; Palolo Valley; BPBM 16435.

Type locality. Hawaiian Islands, Oahu, Nuuanu. See Remarks.

Diagnosis. Shell. Shell dextral, $H = 4.4 \pm 0.18$ mm, $W = 2.7 \pm 0.11$ mm, $WH = 5.1 \pm 0.08$, $AH = 1.9 \pm 0.11$ mm, $AW = 1.3 \pm 0.08$ mm ($N = 50$; Table 2). Whorls inflated. Columella in juveniles with a strong lamella that is reduced and covered by a thickening of the inner edge of the lip in adults. Some adults show a short projection or angulation where the columellar lamella was located. Adult columella reflected, without an axial ridge. Parietal lamella is smooth and not undulate, extending 0.2 to 0.5 whorls into the aperture. Shell color is pale tan or dark brown, with or without a single peripheral color band of pale tan or dark brown (Fig. 3D, MCZ 73037).

Reproductive system. Phallus retractor muscle relatively long, attached apically to a short but well-defined epiphallus (Fig. 4B). Appendix is nearly equal in length to the phallus. Appendix the diameter of the phallus at its attachment, narrowing abruptly at $\frac{1}{3}$ its length and remaining narrow to its terminus. Apical $\frac{3}{4}$ of the phallus is broad, basal $\frac{1}{4}$ narrows abruptly remaining narrow to the junction with the moderately long atrium. Vagina is long and nearly half the length of the phallus.

Radula. Radula with an irregular rachidian flanked on either side by rastriform marginal teeth, as diagnostic of the family (Fig. 5B). Each tooth has a long narrow base that expands slowly for $\frac{3}{4}$ of the length of the tooth before reaching the forward curving cusps, which comprise the remaining $\frac{1}{4}$ of the tooth. There are three long cusps at mesocone, endocone, and ectocone positions with two or more alternating larger and smaller cusps intercalated between them. There are roughly 105 teeth per row ($N = 5$; Table 2).

Distribution and ecology. Auriculella minuta is endemic to Oahu’s Koolau Mountain Range (Fig. 1B), found predominantly in the southern portion of the range with a few historical records from the southern edge of the northern Koolau Mountains. No elevational range information is available with these historical specimen records. The species is arboreal and found on vegetation, including Cordyline fruticosa, Dioscorea alata, Freycinetia arborea, Kadua affinis, Lobelia sp., Psidium guajava, and Touchardia latifolia. Live specimens recorded in the BPBM collection were last collected by Olaf Oswald in Waiahole in 1931 and is considered herein extinct.

Remarks. A holotype was not designated in the original description and the type series came from two different localities: Nuuanu collected by Cooke, and Palolo collected by both Cooke and Lyman (Pilsbry and Cooke 1915: 90). Five figures were provided with the original description (Pilsbry and Cooke 1915: pl. 25, figs 5–9) from Nuuanu, which according to the figure caption were based on specimens from BPBM and ANSP. The figure caption did not indicate which museum lots the figured specimens came from but the BPBM ledger in Cooke's handwriting lists: BPBM 42377 “holotype”, figs 5, 9 (see note for ANSP 91816 below); BPBM 42378, “cotype”,
The first new species of Hawaiian land snail described in 60 years

Figure 4. Comparative reproductive anatomy of A Auriculella auricula BPBM 119141 B Auriculella minuta BPBM 99146 C Auriculella perpusilla BPBM 93626 D Auriculella perversa BPBM 97904 E Auriculella tenella BPBM 211034 F Auriculella gagneorum sp. nov. paratype BPBM 285800. Abbreviations for reproductive structures are: AG = albumen gland; AP = penial appendix; BC = bursa copulatrix; EP = epiphallus; GP = gonopore; P = penis; OV = free oviduct; PG = prostate gland; PR = penial retractor muscle; UT = uterus; VD = vas deferens. Scale bar: 1mm.

fig. 8 (not ANSP 113294 as stated in Severns, 2011: 210); BPBM 42379 “paratypes”; BPBM 42380, “cotype”, fig. 7; BPBM 42381, “paracotypes”; 42382, “cotype”, fig. 6; BPBM 42383, “paracotypes”. The BPBM ledger documents that BPBM lots were the source of other type material: BPBM 42379 – 83 were the source for SMF 7127 (Zilch 1962: 78) and BPBM 42379, split from BPBM 13034, was the source lot for MCZ
73037. The ledger also indicated that two specimens were given to Dautzenberg whose collections were obtained by RBINS. Two ANSP lots 91816 and 113294 were received by Pilsbry from Cooke. The original label for ANSP 91816 is marked “cotype” and the source for fig. 9 in the description. Because the caption for figs 5–9 states that at least one of the figured specimens is from ANSP we believe this to be the source for fig. 9 rather than BPBM 42377 as stated in the BPBM ledger, although we do believe BPBM 42377 is the source for fig. 5. Johnson (1996) lists lot BPBM 42377 as the holotype citing the original BPBM specimen labelling. However, the species description is clearly based on multiple specimens all of which should be considered syntypes. In addition to the specimens from Nuuanu, the material from Palolo collected by both Lyman and Cooke are also part of the type series. There is only one lot of Auriculella minuta (BPBM 12808) collected by Lyman from Palolo and although it is not labelled as being part of the type series it is likely the lot collected by Lyman that was mentioned in the species description. A second lot, BPBM 16435, lacks information on the collector but may be the lot collected by Cooke. We here designate lot BPBM 42377 as the lectotype, restricting the type locality to Nuuanu.

Unlike the other species traditionally placed in the perpusilla group, the shell of A. minuta is dextral rather than sinistral. The columella does not bear an axially oriented ridge like the one found in A. perversa. The palatal lamella is smooth and not undulate unlike that of A. gagneorum sp. nov. The epiphallus is short and well defined similar to A. gagneorum sp. nov., but unlike the long epiphallus of A. perpusilla or the poorly defined epiphallus of A. perversa. The appendix narrows abruptly at approximately ⅓ its length unlike the gently tapered appendix of A. gagneorum sp. nov.

**Auriculella perpusilla E. Smith, 1873**

Figures 1C, 3E, F, 4C, 5C

*Auriculella perpusilla* E. Smith in Gulick & Smith, 1873: 87, pl. 10, fig. 26; Pilsbry and Cooke 1915: 91–92, pl. 25, figs 1, 2; Cowie et al. 1995: 77; Johnson 1996: 193; Severns 2011: 210, pl. 82, fig. 3.

**Type material.** Holotype: USA • 1; shell crushed; H = 4 mm, W = 2 ⅔ mm (according to original description); Honolulu County, Oahu, Koolau Mountains; 1918; John T. Gulick leg.; MCZ 39912.

**Type locality.** “Kohalu” (*sic*, Kahaluu) on Oahu.

**Diagnosis. Shell.** Shell sinistral with inflated whorls, H = 4.4 ± 0.26 mm, W = 3.0 ± 0.15 mm, WH = 5.0 ± 0.14, AH = 2.1 ± 0.14 mm, AW = 1.5 ± 0.11 mm (N = 50; Table 2f). Columella in juveniles with a strong lamella that is reduced and covered by a thickening of the inner edge of the lip in adults. Some adults show a short projection or angulation where the columellar lamella was located. Parietal lamella is smooth and not undulate, extending 0.3 whorls into the aperture, and sometimes bears a weak angulation at mid-point. Shell color is pale tan or dark brown, with or without a single peripheral color band of pale tan or dark brown (Fig. 3F).
**Reproductive system.** Phallus retractor muscle relatively short, attached apically to a long epiphallus, which is nearly 1/3 the length of the phallus (Fig. 4C). Appendix is nearly equal in length to the phallus. Appendix slightly over half the diameter of the phallus at its attachment, narrowing abruptly at 1/6 its length and remaining narrow to its terminus. Apical 2/3 of the phallus is broad, basal 1/3 narrows abruptly and remains narrow to the junction with the short atrium. Vagina is long and nearly half the length of the phallus.

**Radula.** Radula with an irregular rachidian flanked on either side by rastriform marginal teeth, as diagnostic of the family (Fig. 5C). Each tooth has a long narrow base that expands slowly for 3/4 of the length of the tooth before reaching the forward curving cusps, which comprise the remaining 1/4 of the tooth. There are three long cusps at mesocone, endocone, and ectocone positions with two or more alternating larger and smaller cusps intercalated between them. There are roughly 127 teeth per row (N = 5; Table 2).

**Distribution and ecology.** *Auriculella perpusilla* is endemic to Oahu’s Koolau Mountain Range (Fig. 1C), recorded from across the range at elevations of 61 m to 1066 m. The species is arboreal and found on vegetation, including: *Antidesma pulvinatum*, *Cordyline fruticosa*, *Freycinetia arborea*, *Kadua affinis*, *Lobelia* sp., *Metrosideros polymorpha*, *Myrsine* sp., *Psidium guajava*, *Psychotria kaduana*, *Syzygium sandwicense*, *Toucharidia latifolia*, and on unspecified ferns, tree trunks, and dead leaves. Recent observations are restricted to Tantalus (southern Koolau Mountains; Fig. 1C).

**Remarks.** No holotype was designated in the original description which included a single figure and provided a single set of measurements: height 4 mm width 2 2/3 mm. The shell donated by Gulick is MCZ 39912 and is labeled holotype. Pilsbry and Cooke (1915: 91) indicated that only a single shell existed; “The single specimen collected by Mr. Gulick and described by Mr. Smith, is unfortunately broken.” Consequently, MCZ 39912 is the holotype by monotypy.

Unlike *A. minuta*, *A. perpusilla* is sinistral and the columella does not bear an axially oriented ridge like the one found in *A. perversa*. The palatal lamella is smooth and not undulate like *A. gagneorum* sp. nov. The epiphallus is long unlike the poorly defined epiphallus of *A. perversa* or the short but well-defined epiphallus of *A. minuta* and *A. gagneorum* sp. nov. The appendix narrows abruptly at approximately 1/3 its length unlike *A. gagneorum* sp. nov.

*Auriculella perpusilla* Cooke, 1915
Figures 1D, 3G, H, 4D, 5D

*Auriculella perpusilla* Cooke in Pilsbry & Cooke, 1915: 90–91, pl. 25, figs 3, 4; Cowie et al. 1995: 77; Johnson 1996: 193; Severns 2011: 210, pl. 82, fig. 2.

**Type material. Lectotype:** USA • 1; H = 4.7 mm, W = 3.3 mm, AH = 2.2 mm, AW = 2.0 mm, WH = 5.1; Honolulu County, Oahu, Koolau Mountains, Nuuanu; Ridge 9, east side, on *Passiflora foetida*; Cooke leg.; BPBM 42384, here designated.

**Paralectotypes:** USA • 1; Honolulu County, Oahu, Koolau Mountains, Nuuanu; Ridge 9, east side, on *Passiflora foetida*; Cooke leg.; BPBM 42385.
**Paralactotypes not examined:** ANSP 91817 (6 spm), ANSP 108272 (13 spm), ANSP 163399 (1 spm), ANSP 163411 (5 spm), MCZ 73044 (2 spm), SMF 7090 (1 spm).  

**Type locality.** Oahu: Nuuanu. See Remarks.

**Diagnosis. Shell.** Shell sinistral with inflated whorls, $H = 4.4 \pm 0.26$ mm, $W = 3.0 \pm 0.23$ mm, $WH = 5.2 \pm 0.08$, $AH = 2.0 \pm 0.18$ mm, $AW = 1.4 \pm 0.08$ mm (Table 2). Columella in juveniles with a strong lamella that is reduced and covered by a thickening of the inner edge of the lip in adults. The columellar thickening usually bears an axially oriented ridge. Adults do not show a short projection or angulation where the columellar lamella was located. Parietal lamella is smooth and not undulate, extending 0.3 to 0.5 whorls into the aperture. Shell color is solid brown to dark brown with darker brown axial bands (Fig. 3H).

**Reproductive system.** Phallus retractor muscle relatively short attached apically to a short and poorly defined epiphallus (Fig. 4D). Appendix is as long as the phallus and a bit over half the diameter of the phallus at its attachment, narrowing abruptly at ⅓ its length and remaining narrow to its terminus. Phallus is broad, narrowing only slightly at the junction with the short atrium. Vagina is short.

**Radula.** Radula with an irregular rachidian flanked on either side by rastriform marginal teeth, as diagnostic of the family (Fig. 5D). Each tooth has a long narrow base that expands slowly for ¾ of the length of the tooth before reaching the forward curving cusps, which comprise the remaining ¼ of the tooth. There are three long cusps at mesocone, endocone, and ectocone positions with two or more alternating larger and smaller cusps intercalated between them. There are roughly 127 teeth per row ($N = 4$; Table 2).

**Distribution and ecology.** *Auriculella perversa* is endemic to Oahu's southern Koolau Mountain Range (Fig. 1D), recorded from 61 m to 914 m elevation. *Auriculella perversa* is arboreal and found on *Clermontia* sp., *Cordyline fruticosa*, *Dubautia laxa*, *Freycinetia arborea*, *Metrosideros polymorpha*, *Musa* sp., *Pritchardia* sp., *Psidium guajava*, and unspecified ferns, tree trunks, and dead leaves. Prior to our recent surveys the last live specimens were collected in 1939 by O.H. Emerson, E.H. Bryan Jr., and D. Anderson on Kulepeamo Ridge in the southern Koolau Mountain Range, and the only known extant population recorded occurs in Tantalus.

**Remarks.** A holotype was not designated in the original description and the type series came from two different localities: Nuuanu collected by Cooke, and Kuliouou collected by Thaanum. Two figures were provided with the original description (Pilsbry and Cooke 1915: pl. 25, figs 3, 4) for material from Nuuanu at BPBM. However, the figure caption does not indicate type status or lot numbers. The BPBM ledger in Cooke’s handwriting lists: BPBM 42384 “holotype”, figs 3, 4; BPBM 42385, “paratypes”. The BPBM ledger documents that BPBM 42385 was also the source of MCZ 7034 and SMF 7090 (Zilch, 1962: 78). The ANSP online catalog list additional specimens from BPBM and labeled as syntypes: ANSP 163411, 91817, Nuuanu; ANSP 163399 Kuliousu [sic]. ANSP 108272 Kuliouou was collected by D. Thaanum. Johnson (1996: 193) stated that the “holotype” was BPBM 42384 based on its specimen label. However, it is clear that the original description was based on multiple specimens which should be considered syntypes. We here designate BPBM 42384 as the lectotype. As a result of this lectotype designation the type locality is restricted to Nuuanu.
The first new species of Hawaiian land snail described in 60 years

Figure 5. Comparative radular morphology of A. auricula (irregular rachidian and rastriform marginal teeth) B. auricula (rastriform marginal teeth) C. minuta (rastriform marginal teeth) D. perpusilla (irregular rachidian and rastriform marginal teeth) E. perversa (rastriform marginal teeth) F. tenella (rastriform marginal teeth) G. gagneorum sp. nov. (irregular rachidian and rastriform marginal teeth) H. gagneorum sp. nov. (rastriform marginal teeth). Scale bar: 10 µm.

Unlike A. minuta, the shell of A. perversa is sinistral. The columella bears an axially oriented ridge unlike all other species in the perpusilla group. The palatal lamella is smooth and not undulate like A. gagneorum sp. nov. The reproductive system includes a short and poorly defined epiphallus and an appendix that narrows abruptly at ap-
proximately ⅓ its length. The epiphallus is short and poorly defined unlike the long epiphallus of *A. perpusilla* or the short but well-defined epiphallus of *A. minuta* and *A. gagneorum* sp. nov.

*Auriculella tenella* Ancey, 1889
Figures 1E, 3I, J, 4E, 5E

*Auriculella tenella* Ancey, 1889: 232–233; Pilsbry and Cooke 1915: 99–100, pl. 19, figs 7, 8; Cowie et al. 1995:77; Wood and Gallichan 2008: 88, pl. 2, fig. 8, ix; Severns 2011: 204, pl. 79, fig. 5.

**Type material.** *Lectotype*: USA • 1; H = 6.2 mm, W = 3.5 mm, AH = 2.3 mm, AW = 1.6 mm, WH = 6.6 whors; Honolulu County, Oahu, Waianae Mountains; Baldwin leg.; BPBM 18943, here designated.

*Paralectotypes*: USA • 2; Honolulu County, Oahu, Waianae Mountains; Baldwin leg.; BPBM 285811.

*Paralectotypes not examined*: NMW 1955.158.24126 (1 spm); RBINS 10591 (accession, 1 spm).

**Type locality.** “Waianae, dans la partie occidentale de l’île d’Oahu.” [Waianae, western part of Oahu Island].

**Diagnosis. Shell.** Shell sinistral with inflated whors, H = 5.6 ± 0.8 mm, W = 3.0 ± 0.4 mm, WH = 6.5 ± 0.3, AH = 2.0 ± 0.3 mm, AW = 1.9 ± 0.3 mm (N = 50; Table 2). Columella in juveniles with two lamellae that are reduced and visible only deep within the aperture of adults. Columellar reflection lacks an axially oriented ridge. Parietal lamella is smooth and not undulate, extending 0.3 to 0.5 whors into the aperture. Shell color straw to brown, indistinctly streaked with red, with or without a single darker brown marginal spiral band.

**Reproductive system.** Phallus retractor muscle relatively long attached apically to a short but well-defined epiphallus (Fig. 4E). Appendix ⅓ longer and about half the diameter of the phallus at its attachment, narrowing abruptly at ⅓ its length and remaining narrow to its terminus. Phallus is broad, narrowing by half at the junction with the short atrium. Vagina is of moderate length.

**Radula.** Radula with an irregular rachidian flanked on either side by rastiform marginal teeth, as diagnostic of the family (Fig. 5E). Each tooth has a long narrow base that expands slowly for ¾ of the length of the tooth before reaching the forward curving cusps, which comprise the remaining ¼ of the tooth. There are three long cusps at mesocone, endocone, and ectocone positions with two or more alternating larger and smaller cusps intercalated between them. There are roughly 129 teeth per row (N = 3; Table 2).

**Distribution and ecology.** *Auriculella tenella* is endemic to Oahu’s Waianae Mountains, historically found throughout the range between 518 and 1227 m in elevation (Fig. 1E). This species is arboreal and found on *Broussaisia* sp., *Cordyline* sp., *Freycinetia arborea*, *Lantana* sp., *Pelea* sp., *Sadleria cyatheoides*, *Bidens* sp., *Coprosma* sp.,
The first new species of Hawaiian land snail described in 60 years

**Euphorbia** sp., *Metrosideros* sp., *Psychotria* sp., *Ilex* sp., *Philodendron* sp., and unspecified ferns, grasses, tree trunks, and small plants on stream banks. Occasionally, this species has been recorded on the ground on stones, dead leaves, and bark. The last live specimens in the BPBM collection were recorded in 1948. Our recent surveys documented the species in only three locations in the southern Waianae range.

**Remarks.** A holotype was not designated in the original description, however, the type locality is listed as “Waianae” and collected by Baldwin. Ancey provided measurements in the original description, “Long., 6; diam., 3; alt. ap., 2 2/3 millim.”, which agree well with the designated lectotype. The ledger entry for BPBM 18943 lists four “types” collected by Baldwin from Waialae [sic]. However, only three specimens were found. The material probably came from Paul Geret who acquired Ancey’s collection after his death and subsequently sold it. Much of Ancey's Hawaiian land and freshwater material was purchased by BPBM in 1908 (Johnson, 1996) but some was sold to other buyers. Both NMW 1955.158.24126 and RBINS 10591 (accession number) have Geret “cotype” labels (Wood and Gallichan 2008:88). Tomlin, the source of the NMW lot, had a sales list confirming purchase from the Ancey collection.

The shell of *A. tenella* has approximately seven nearly flat-sided whorls unlike *A. auricula*, *A. minuta*, *A. perpusilla* and *A. perversa*, which have approximately five whorls, and are inflated in all but *A. auricula*. *Auriculella tenella* is sinistral unlike *A. minuta* and does not bear an axially oriented columellar ridge like *A. perversa* or an undulating palatal lamella like *A. gagneorum* sp. nov. The epiphallus is short and well defined unlike the long epiphallus of *A. perpusilla* or the poorly defined epiphallus of *A. perversa*. The appendix narrows abruptly at approximately ½ its length unlike *A. gagneorum* sp. nov.

**Auriculella gagneorum** sp. nov.

http://zoobank.org/25f68bf8-12f1-461e-be17-263982427bb0

Figures 1F, 3K, L, 4F, 5F, 6A-C

**Material examined. Holotype:** USA • 1, H = 4.7 mm, W = 3.4 mm, AH = 2.3 mm, AW = 1.8 mm, WH = 5.3 whorls; Honolulu County, Oahu, Waianae Mountains, Palawai Gulch; 710 m; 9 Feb. 2018; K. A. Hayes, N. W. Yeung, J. Slapcinsky; hand collected on *Pisonia umbellifera*; GenBank: MT519824-MT519826, MT519866-MT519868, MT519889-MT519952; BPBM 285843.

**Paratypes:** USA – Honolulu County, Oahu, Waianae Mountains • 1; Puu Hapapa; 23 Jan 2013; D.T.A. Gary, K. Leung, D. R. Sischo, V. J. Costello; BPBM 285794 • 8; Puu Hapapa; 23 Jan 2013; D.T.A. Gary, K. Leung, D. R. Sischo, V. J. Costello; BPBM 285795 • 1; Palawai; 24 Dec 2014; D. R. Sischo and SEPP crew; BPBM 285799 • 3; Puu Hapapa; 24 Jan 2013; D.T.A. Gary, K. Leung, D. R. Sischo, V. J. Costello; BPBM 285796 • 2; Ekahanui; 17 Feb 2013; D.T.A. Gary, K. Leung, D. T. B. Ressler, V. J. Costello; BPBM 285797 • 1; Palawai; 24 Dec 2014; D. R. Sischo and SEPP crew; BPBM 285798 • 2; Palawai; 24 Dec 2014; D. R. Sischo and SEPP crew; BPBM 285800.
**Figure 6.** Photographs of live animals of *Auriculella gagneorum* sp. nov. **A** eggs **B** 1-day old juveniles **C** adult. Scale bars: 1 mm.

**Other material:** USA – Honolulu County, Oahu, Waianae Mountains • 37; Palikea Ridge; 12 October 1912; R. von Holt, Cooke; BPBM 24989 • 44; Palikea Ridge; 12 October 1912; von Holt, Cooke; BPBM 33011 • 27; Palikea Ridge; 12 October 1912; von Holt, Cooke; BPBM 33018 • 10; Palikea Ridge; 12 October 1912; von Holt, Cooke; BPBM 33006 • 3; Makua; 16 November 1913; Spalding; BPBM 34847 • 3; Palikea Ridge; 27 December 1914; Alice T. Cooke, C.M. Cooke; BPBM 38031 • 79; Palikea Ridge; 24 August 1922; R. von Holt, C.M. Cooke Jr., M.C. Neal; BPBM 59612 • 11; Napepeiauolelo; 25 March 1934; Meinecke, William H.; BPBM 127221 • 1; Palawai Gulch; 30 August 1935; D’Alte A. Welch, Glen W. Russ; BPBM 174037 • 15; Palawai Gulch; 30 August 1935; Glen W. Russ, D’Alte A. Welch; BPBM 174233 • 2; Palawai Gulch; 30 August 1935; D’Alte A. Welch, Glen W. Russ; BPBM 174141 • 3; Palawai Gulch; 30 August 1935; D’Alte A. Welch, Glen W. Russ; BPBM 174081 • 1; Manuwaikaalae Gulch; 28 March 1936; J. Winne, D’Alte A. Welch; BPBM 176456 • 2; Pohakea Gulch; 30 March 1936; J. Winne, D’Alte A. Welch; BPBM 176596 • 3; Pualii Gulch; 30 March 1936; J. Winne, D’Alte A. Welch; BPBM 176651 • 21; Pualii Gulch; 30 March 1936; J. Winne, D’Alte A. Welch; BPBM 176766 • 1; Kaaikukai Gulch; 03 April 1936; B. Bowen, D’Alte A. Welch; BPBM 176916 • 11; Kaaikukai; 03 April 1936; B. Bowen, D’Alte A. Welch; BPBM 176973 • 15; Palawai Gulch; 19...
The first new species of Hawaiian land snail described in 60 years

April 1936; J. Winne, D’Alte A. Welch; BPBM 177217 • 9; Palawai Gulch; 19 April 1936; J. Winne, D’Alte A. Welch; BPBM 177278 • 1; Kaaiukukai Gulch; 05 May 1936; R. Yamaguchi, D’Alte A. Welch; BPBM 177468 • 1; Mount Kaala; 27 March 1937; F. Raymond Fosberg; BPBM 162712 • 11; Napepeiauolelo; 03 April 1938; William H. Meinecke, E. Meadows, Donald Anderson; BPBM 173979 • 9; Napepeiauolelo; 03 April 1938; William H. Meinecke, E. Meadows, Donald Anderson; BPBM 173980 • 2; Pualii Gulch; 03 April 1938; William H. Meinecke, E. Meadows, Donald Anderson; BPBM 184885 • 5; Ekahanui Gulch; 16 September 1941; Rokuro Yamaguchi, Yoshio Kondo; BPBM 211563 • 2; Ekahanui Gulch; 16 September 1941; Rokuro Yamaguchi, Yoshio Kondo; BPBM 211678 • 6; Ekahanui Gulch; 16 September 1941; Rokuro Yamaguchi, Yoshio Kondo; BPBM 211723 • 5; Napepeiauolelo-Pualii Ridge; 15 October 1960; Yoshio Kondo, T.M. {T. Maa?}, George F. Arnemann, P.C. {Peter Char?}; BPBM 216123 • 2; Palawai Gulch; BPBM 183862 • 135; Palikea Ridge; R. von Holt, Cooke; BPBM 21823 • 17; Palikea Ridge; R. von Holt, Cooke; BPBM 21824 • 74; Palikea Ridge; Spalding; BPBM 22739 • 6; Palikea Ridge; Spalding; BPBM 19891 • 1; Palikea Ridge; Cooke; BPBM 16884.

Type locality. Palawai Gulch, Waianae Mountains, Honolulu County, Oahu

Diagnosis. Shell. Shell sinistral with inflated whorls, H = 4.8 ± 0.3 mm, W = 3.2 ± 0.2 mm, WH = 5.4 ± 0.4, AH = 2.3 ± 0.1 mm, AW = 1.7 ± 0.1 mm (Table 2). Columella in juveniles with a strong lamella that is reduced and covered by a thickening of the inner edge of the lip in adults. Adults do not show a short projection or angular edge where the columellar lamella was located. Parietal lamella is often undulate, usually with three peaks, extending 0.2 to 0.5 whorls into the aperture. Shell color is white, pale tan or dark brown, with or without irregularly placed axial bands of brown, or with a single peripheral band of pale tan or dark brown. Specimens occasionally pale tan with two poorly defined dark bands on either side of a pale tan peripheral band.

Reproductive system. Phallus retractor muscle long, attached apically to a short but well-defined epiphallus (Fig. 4F). Appendix slightly longer than the phallus. Appendix ⅔ the diameter of the phallus at its attachment, tapering gently to ⅓ its length, then remaining narrow to its terminus. Apical ⅔ of the phallus is broad, tapering slightly both apically and basally, basal ¼ narrows slightly above junction with the short atrium. Vagina is short.

Radula. Radula with an irregular rachidian flanked on either side by rastriform marginal teeth, as diagnostic of the family (Fig. 5F). Each tooth has a long narrow base that expands slowly for ¾ of the length of the tooth before reaching the forward curving cusps, which comprise the remaining ¼ of the tooth. There are three long cusps at mesocone, endocone, and ectocone positions with two or more alternating larger and smaller cusps intercalated between them. Number of teeth per row range from 135 to 153 (N = 3; Table 2).

Distribution and ecology. Auriculella gagneorum sp. nov. is endemic to Oahu’s Waianae Mountain Range and was recorded as a potentially new species primarily from the southern Waianae Mountain Range, with several populations in the northern
part of the range (Fig. 1F). The species is arboreal and has been found on Antidesma platyphyllum, Broussaisia arguta, Lantana sp., Melicope anisate, Myrsine lessertiana, and occasionally on unspecified ferns and dead leaves. The last known record of this species prior to recent surveys was by Yoshio Kondo, T. Maa, George F. Arnemann, and Peter Char in 1960. From 2013 to 2018 we recorded extant populations of this species from three locations in the southern Waianae Mountains.

Remarks. The shell is sinistral unlike A. minuta and the columella does not bear an axially oriented ridge like the one found in A. perversa. The palatal lamella is often undulate unlike all other members of the A. perpusilla group. The epiphallus is short but well defined similar to A. minuta but unlike the long epiphallus of A. perpusilla or the poorly defined epiphallus of A. perversa. The appendix tapers gently unlike the appendices of A. auricula, A. minuta, A. perpusilla, A. perversa, and A. tenella which all narrow abruptly.

Etymology. Named in honor of Betsy and Wayne Gagne for their indefatigable efforts advocating for the conservation of Hawaii’s unique and highly endangered biota.

Discussion

The Auriculella perpusilla species group (A. perpusilla, A. perversa, A. minuta) was defined as having species with small, thin, relatively low spired shells of approximately five inflated whors. Auriculella gagneorum sp. nov., shares these shell characteristics. These four species can be distinguished from one another using a suite of morphological features including shell chirality (only A. minuta is dextral); presence of axially oriented ridge of the columella (only present in A. perversa); appearance of the palatal lamella (undulated only in Auriculella gagneorum sp. nov.); length of the epiphallus (those of both Auriculella gagneorum sp. nov. and minuta are short and well-defined); and development of the appendix (tapers gently in Auriculella gagneorum sp. nov. and narrow abruptly in others). The DNA data corroborate the difference seen in anatomy and conchology. In contrast to expectations based on shell morphology alone, the perpusilla group is not monophyletic and Auriculella gagneorum sp. nov. is not closely related to either A. perpusilla or A. perversa, the only other extant members of the group for which DNA data are available (Fig. 2). Instead, A. gagneorum sp. nov. clusters with A. tenella, a high spired and tightly coiled species from the castanea group, which also occurs in the Waianae Mountains. Similarly, A. perpusilla and A. perversa are more closely related to species with highly dissimilar shell morphologies, A. ambusta and A. montana, respectively (Fig. 2). The latter two have large, thick shells and are usually placed in the auricula group with other robust species. Patterns of relatedness recovered in our phylogenetic analyses indicate these gross shell characters, which are unlikely to be independent of one another, are insufficient for delineating taxa or characterizing relationships within the genus. Multiple instances of convergence in shell morphology across the genus may be explained by adaptation to similar microhabitats, or non-adaptive diversification combined with constraints on shell morphospace (Gittenberger 1991; Cowie 1995; Rundell and Price 2009; Chiba and Cowie 2016;
The first new species of Hawaiian land snail described in 60 years (Gillespie et al. 2018). Disentangling the processes responsible for these patterns will require additional studies of the functional morphology, ecology, and behavior of Auriculella species.

Historically, all four species treated here once had much larger geographic ranges, with multiple populations recorded in the last century (Fig. 1). Like nearly all land snail species across Hawaii, Auriculella spp. numbers have declined dramatically with an estimated 45% of the species considered extinct, and many historical populations extirpated as a result of habitat destruction, invasive species, and possibly climate change. Despite the grim statistics, there remain a number of species that can yet be saved from extinction, but only with a clear understanding of their systematics, biogeography and ecology. For example, A. tenella, A. gagneorum sp. nov., A. perversa, and A. perpusilla, are now known from only three locations for each of these species. These data combined with knowledge of reproduction and population growth rates can be used to better manage these imperiled species.

Low reproductive and growth rates are often characteristic of species that have evolved on isolated oceanic islands (MacArthur and Wilson 2001; Covas 2011), and Auriculella spp. are probably no exception. Two laboratory reared adults of Auriculella gagneorum sp. nov. produced 33 eggs in 250 days between 17 May 2018 and 23 January 2019 (Fig. 6A–C). The delicate nature of the eggs of this imperiled species permitted the measurement of only three eggs, which had an average diameter of 0.99 ± 0.05 mm. These large eggs, relative to the size of the animal, take approximately 58 days to hatch (Lindsay Renshaw, pers comm.). Such low fecundity in combination with extreme range reduction decreases the chances of long-term species and population persistence (Bick et al. 2018), particularly in the face of predation by introduced predators (Chiba and Cowie 2016).

Updated and comprehensive assessments of the systematics, biogeography, and ecology of taxa are necessary for effective management and development of long-term recovery plans. Additional surveys to locate remaining species and persisting populations are needed now, while there is still an opportunity to prevent or slow the rate of species loss (Solem 1990; Yeung and Hayes 2018). These surveys provide important opportunities to study and preserve species and develop populations for captive rearing, which in turn can be repatriated to protective enclosures in natural habitats with the goal of ultimately reintroducing species back into the wild (Natural Area Reserves Program 2016; Yeung and Hayes 2018). Our surveys have recovered species not recorded alive since the 1950s (e.g., Auriculella perpusilla, A. perversa, A. tenella) and others feared extinct (Yeung et al. 2015, 2018). They have also uncovered several previously undescribed species, indicating that there is still much to learn about this highly imperiled fauna, and still hope that we might save some of it for future generations (Solem 1990).

Acknowledgements

We thank Angela Nishimoto, Kelli DeLeon, Connor Kalahiki, Lily Evans, Anna Elazar, and Miriam Lipman for databasing the BPBM Auriculella collection, and Lynette
Williams for her dedication in scanning of the Museum’s ledgers. We are thankful for Dr. Tricia Goulding’s assistance in assessing type material and imaging of specimens along with Dylan Ressler and Kelley Leung. We are indebted to Drs. Carl Christensen, Robert Cowie, and Daniel Chung for all the support and encouragement they have provided the authors over the years and their guidance and substantial contributions to research and conservation of Hawaiian land snails. Many thanks to Scott Whitaker (Scientific Imaging, National Museum of Natural History, Smithsonian Institution) for helping with the scanning electron micrographs. We are grateful to Vincent Costello (OANRP), Jamie Tanino (OANRP), David Sischo (DLNR), Keahi Bustamente (DLNR) and their teams for their dedication to conservation in Hawaii, and particularly for their assistance in field surveys during the last decade. Additionally, much mahalo to Pomaikai Kaniaupio-Crozier (Puu Kukui Watershed), Lance DeSilva (DLNR), Fern Duvall (DLNR), Randy Bartlett (PKW, EMWP, DLNR), and the East Maui Watershed crew, who provided logistical support and helped with permission to access land in their care. We very much appreciate Drs. Mike Hadfield, David Sischo, Thierry Backeljau, and an anonymous reviewer for providing suggestions that improved the manuscript. We appreciate the support of David Hayes in all our work. All collections were approved under DLNR scientific permits for native invertebrate research and special use permit for the Natural Area Reserves System. Funding for Hawaiian land snail research and this project were provided by NSF (DBI-1902328, DEB-1656231, DBI-1561774, to NWY, KAH and JS; DEB1120906 to KAH). This is Contribution No. 2020-004 to Bishop Museum Hawaii Biological Survey.

References

Ancey CF (1889) Étude sur la faune malacologique des Iles Sandwich. Bulletins de la Société Malacologique de France 6: 171–258. https://doi.org/10.5962/bhl.title.13081

Bick CS, Pearce-Kelly P, Coote T, Ó Foighil D (2018) Survival among critically endangered partulid tree snails is correlated with higher clutch sizes in the wild and higher reproductive rates in captivity. Biological Journal of the Linnean Society 125 (3): 508–520. https://doi.org/10.1093/biolinnean/bly124

Bouchet P, Rocroi JP, Hausdorff B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61(1–2): 1–526. https://doi.org/10.4002/040.061.0201

Cardoso P, Erwin TL, Borges PAV, New TR (2011) The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation 144 (11): 2647–2655. https://doi.org/10.1016/j.biocon.2011.07.024

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17(4): 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Chernomor O, von Haeseler A, Minh BQ (2016) Terrace aware data structure for phylogenomic inference from supermatrices. Systematic Biology 65(6): 997–1008. https://doi.org/10.1093/sysbio/syw037
The first new species of Hawaiian land snail described in 60 years

Chiba S (2009) Morphological divergence as a result of common adaptation to a shared environment in land snails of the genus Hirasea. Journal of Molluscan Studies 75(3): 253–259. https://doi.org/10.1093/mollus/eyp020

Chiba S, Cowie RH (2016) Evolution and extinction of land snails on oceanic islands. Annual Review of Ecology, Evolution, and Systematics 47: 123–141. https://doi.org/10.1146/annurev-ecolsys-112414-054331

Cowie CM, Kondo Y (1960) Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). Bernice P. Bishop Museum Bulletin 221: 1–303. http://hbs.bishopmuseum.org/pubs-online/pdf/bull221.pdf

Cowie RH (1995) Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. Evolution 49(6): 1191–1202. https://doi.org/10.10111/j.1558-5646.1995.tb04446.x

Cowie RH, Evenhuis NL, Christensen CC (1995) Catalog of the native land and freshwater molluscs of the Hawaiian Islands. Backhuys Publishers, Leiden, 248 pp.

Covas R (2011) Evolution of reproductive life histories in island birds worldwide. Proceedings of the Royal Society B: Biological Sciences 279(1733): 1531–1537. https://doi.org/10.1098/rspb.2011.1785

Durkan TH, Yeung, NW, Meyer WM, Hayes KA, Cowie RH (2013) Evaluating the efficacy of land snail survey techniques in Hawaii: implications for conservation throughout the Pacific. Biodiversity and Conservation 22(13–14): 3223–3232. https://doi.org/10.1007/s10531-013-0580-7

Erickson PB, Hadfield MG (2008) Isolation and characterization of eight polymorphic microsatellite loci in the endangered Hawaiian tree snail, Achatinella sowerbyana. Molecular Ecology Resources 8(4): 808–810. https://doi.org/10.1111/j.1755-0998.2007.02071.x

Férussac AEJ (1821) Tableaux systématiques des animaux mollusques classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; suivis d’un Prodrome général pour tous les mollusques terrestres ou fluviatiles vivants ou fossiles. Première partie, Tableaux systématiques généraux, i-xlvi. Deuxième partie, 2, Tableau de la famille des limaçons, 92 pp. https://www.biodiversitylibrary.org/page/11057235

Fukuda H, Haga T, Tatara Y (2008) Niku-nuki: a useful method for anatomical and DNA studies on shell-bearing molluscs. Zoosymposia 1: 15–38. https://doi.org/10.11646/zoosymposia.1.1.5

Gillespie RG, Benjamin SP, Brewer MS, Rivera MAJ, Roderick GK (2018) Repeated diversification of ecomorphs in Hawaiian stick spiders. Current Biology 28(6): 941–947. https://doi.org/10.1016/j.cub.2018.01.083

Gittenberger E (1991) What about non-adaptive radiation? Biological Journal of the Linnean Society 43(4): 263–272. https://doi.org/10.1111/j.1095-8312.1991.tb00598.x

Gulick JT (1872) On the variation of species as related to their geographical distribution, illustrated by the Achatinellinae. Nature 6: 222–224. https://doi.org/10.1038/006222b0

Gulick JT (1873) On the classification of the Achatinellinae. Proceedings of the Zoological Society of London 1873: 89–91. https://www.biodiversitylibrary.org/page/28504282

Gulick JT, Smith EA (1873) Descriptions of new species of Achatinellinae. Proceedings of the Zoological Society of London 1873: 73–89. https://www.biodiversitylibrary.org/page/28504266
Hadfield MG, Miller SE, Carwile AH (1993) The decimation of endemic Hawai’ian tree snails by alien predators. American Zoologist 33(6): 610–622. https://doi.org/10.1007/s10530-008-9409-9

Hadfield MG, Sauffer JE (2009) The demographics of destruction: isolated populations of arboreal snails and sustained predation by rats on the island of Moloka’i 1982–2006. Biological Invasions 11(7): 1595–1609. https://doi.org/10.1007/s10530-008-9409-9

Holland BS, Hadfield MG (2002) Islands within an island: phylogeography and conservation genetics of the endangered Hawaiian tree snail Achatinella mustelina. Molecular Ecology 11(3): 365–385. https://doi.org/10.1046/j.1365-294X.2002.01464.x

Holland BS, Hadfield MG (2004) Origin and diversification of the endemic Hawaiian tree snails (Achatinellidae: Achatinellinae) based on molecular evidence. Molecular Phylogenetics and Evolution 32(2): 588–600. https://doi.org/10.1016/j.ympev.2004.01.003

Holland BS, Hadfield MG (2007) Molecular systematics of the endangered O’ahu tree snail Achatinella mustelina: synonymization of subspecies and estimation of gene flow between chiral morphs. Pacific Science 61(1): 53–66. https://doi.org/10.1353/psc.2007.0007

Johnson RI (1996) Types of land and freshwater mollusks from the Hawaiian Islands in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology 155(4): 159–214. https://www.biodiversitylibrary.org/page/4272327

Kalyaanamoorthy S, Minh BQ, Wong TK, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14(6): 587–589. https://doi.org/10.1038/nmeth.4285

Kazutaka K, Standle DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability, Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

MacArthur RH, Wilson EO (2001) The Theory of Island Biogeography (Vol. 1). Princeton University Press, Princeton, 203 pp. https://doi.org/10.1515/9781400881376

Meier R, Shiyang K, Vaidya G, Ng PK (2006) DNA barcoding and taxonomy in Diptera: a tale of high intraspecific variability and low identification success. Systematic Biology 55(5): 715–728. https://doi.org/10.1080/10635150600969864

Natural Area Reserves System Hawaii (2016) Pahole Natural Area Reserve Management Plan. Department of Land and Natural Resources, Honolulu, 80 pp. https://dlnr.hawaii.gov/ecosystems/files/2016/10/PaholeDraftManagementPlan.pdf

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2014) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

Odhner NH (1922) Mollusca from Juan Fernandez and Easter Island. In: Skottsberg C (Ed.) The Natural History of Juan Fernandez and Easter Island (Vol. 3). Zoology, Almqvist & Wiksells, Uppsala, 219–254. https://www.biodiversitylibrary.org/page/20632859

O’Rorke R, Cobian GM, Holland BS, Price MR, Costello V, Amend AS (2015) Dining local: the microbial diet of a snail that grazes microbial communities is geographically structured. Environmental Microbiology 17(5): 1753–1764. https://doi.org/10.1111/1462-2920.12630

Rundell RJ, Price TD (2009) Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. Trends in Ecology and Evolution 24(7): 394–399. https://doi.org/10.1016/j.tree.2009.02.007
The first new species of Hawaiian land snail described in 60 years

Palumbi SR (1996) Nucleic acids II: The polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK (Eds) Molecular Systematics. Sinauer Associates, Inc, Sunderland, 205–247.
Pfeiffer L (1855) Descriptions of twenty-seven new species of Achatinella, from the collection of H. Cuming, Esq., collected by Dr. Newcomb and by Mons. D. Frick, late consul-general of France at the Sandwich Islands. Proceedings of the Zoological Society of London 23: 1–7. https://www.biodiversitylibrary.org/page/30747832
Pilsbry HA, Cooke CM (1914–1916) Manual of Conchology. Second Series: Pulmonata (Vol. XXIII). Academy of Natural Sciences, Philadelphia, 302 pp. https://www.biodiversitylibrary.org/page/1296750
Price MR, Forsman ZH, Knapp I, Hadfield MG, Toonen RJ (2016) The complete mitochondrial genome of Achatinella mustelina (Gastropoda: Pulmonata: Stylommatophora). Mitochondrial DNA Part B 1(1): 175–177. https://doi.org/10.1080/23802359.2016.1149787
Price MR, Forsman ZH, Knapp IS, Toonen RJ, Hadfield MG (2016) The complete mitochondrial genome of Achatinella souerbyana (Gastropoda: Pulmonata: Stylommatophora: Achatinellidae). Mitochondrial DNA Part B 1: 666–668. https://doi.org/10.1080/23802359.2016.1219631
Price MR, Forsman ZH, Knapp I, Toonen RJ, Hadfield MG (2018) A comparison of mitochondrial genomes from five species in three genera suggests polyphyly in the subfamily Achatinellinae (Gastropoda: Pulmonata: Stylommatophora: Achatinellidae). Mitochondrial DNA Part B 3(2): 611–612. https://doi.org/10.1080/23802359.2018.1473737
Price MR, Sischo D, Pascua MA, Hadfield MG (2015) Demographic and genetic factors in the recovery or demise of ex situ populations following a severe bottleneck in fifteen species of Hawaiian tree snails. PeerJ 3: e1406. https://doi.org/10.7717/peerj.1406
Régnier C, Fontaine B, Bouchet P (2009) Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. Conservation Biology 23(5): 1214–1221. https://doi.org/10.1111/j.1523-1739.2009.01245.x
Régnier C, Bouchet P, Hayes KA, Yeung NW, Christensen CC, Chung DJ, Fontaine B, Cowie RH (2015) Extinction in a hyperdiverse endemic Hawaiian land snail family and implications for the underestimation of invertebrate extinction. Conservation Biology 29(6): 1715–1723. https://doi.org/10.1111/cobi.12565
Schilthuizen M, van Til A, Salverda M, Liew TS, James SS, bin Elahan B, Vermeulen JJ (2006) Microgeographic evolution of snail shell shape and predator behavior. Evolution 60(9): 1851–1858. https://doi.org/10.1111/j.0011-0429.2006.tb00528.x
Severns M (2009) A new species of Newcombia from the Pleistocene of Kaua‘i, Hawaiian Islands, USA (Gastropoda, Pulmonata, Achatinellidae). Basteria 73(1/3): 57–60. http://natuurtijdschriften.nl/record/597355
Severns M (2011) Shells of the Hawaiian Islands – the Land Shells. ConchBooks, Hackenheim, 460 pp.
Sischo DR, Price MR, Pascua MA, Hadfield MG (2016) Genetic and demographic insights into the decline of a captive population of the endangered Hawaiian tree snail Achatinella fuscobasis (Achatinellidae). Pacific Science 70(2): 133–141. https://doi.org/10.2984/70.2.1
Slapcinsky J, Kraus F (2016) Revision of Partulidae (Gastropoda, Stylommatophora) of Palau, with description of a new genus for an unusual ground-dwelling species. ZooKeys 614: 27–49. https://doi.org/10.3897/zookeys.614.8807
Solem A (1976) Endodontoid Land Snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part. 1: Family Endodontidae. Field Museum of Natural History, Chicago, 508 pp. https://doi.org/10.5962/bhl.title.2554

Solem A (1977) Fossil endodontid land snails from Midway Atoll. Journal of Paleontology 51(5): 902–911. https://www.jstor.org/stable/1303762

Solem A (1984) A world model of land snail diversity and abundance. In: Solem A, van Bruggen AC (Eds) World-Wide Snails: Biogeographical Studies on Non-Marine Mollusca. Brill/Backhuys, Leiden, 6–22.

Solem A (1990) How many Hawaiian land snail species are left? And what we can do for them. Bishop Museum Occasional Papers 30: 27–40. http://hbs.bishopmuseum.org/pubs-online/pdf/op30p27.pdf

Thacker RW, Hadfield MG (2000) Mitochondrial phylogeny of extant Hawaiian tree snails (Achatinellinae). Molecular Phylogenetics and Evolution 16(2): 263–270. https://doi.org/10.1006/mpev.2000.0793

Wade CM, Mordan PB, Naggs F (2006) Evolutionary relationships among the Pulmonate land snails and slugs (Pulmonata, Stylommatophora). Biological Journal of the Linnean Society 87(4): 593–610. https://doi.org/10.1111/j.1095-8312.2006.00596.x

Wood H, Gallichan J (2008) The new molluscan names of César-Marie-Felix Ancey including illustrations of type material from the National Museum of Wales. Studies in Biodiversity and Systematics of Terrestrial Organisms from the National Museum of Wales. Biotir Reports 3: 1–162.

Yeung NW, Bustamente KM, Sischo DR, Hayes HA (2018) Rediscovery of Newcombia canaliculata (Baldwin, 1895) (Gastropoda: Achatinellidae) and Laminella venusta (Mighels, 1845) (Gastropoda: Amastridae). Bishop Museum Occasional Papers 123: 31–36. http://hbs.bishopmuseum.org/pubs-online/pdf/op123p31-36.pdf

Yeung NW, Chung D, Sischo DR, Hayes KA (2015) Rediscovery of Auriculella pulchra Pease, 1868 (Gastropoda: Pulmonata: Achatinellidae). Bishop Museum Occasional Papers 116: 49–51. http://hbs.bishopmuseum.org/pubs-online/pdf/op116p49-51.pdf

Yeung NW, Cowie RH, Hayes KA, Strong EE (2017) Type specimens of Hawaiian land snails in the Smithsonian Institution, National Museum of Natural History, with lectotype designations. Smithsonian Contributions to Zoology 647: 1–34. https://doi.org/10.5479/si.1943-6696.647

Yeung NW, Hayes KA (2018) Biodiversity and extinction of Hawaiian land snails: how many are left now and what must we do to conserve them—a reply to Solem. Integrative and Comparative Biology 58(6): 1157–1169. https://doi.org/10.1093/icb/icy043

Zilch A (1962) Die Typen und Typoide des Natur-Museums Senckenberg, 26: Mollusca, Achatinellacea. Archiv für Molluskenkunde 91: 77–94.
Supplementary material I

Non-type material examined for *Auriculella auricula, A. minuta, A. perpusilla, A. perversa, and A. tenella*
Authors: Norine W. Yeung, John Slapcinsky, Ellen E. Strong, Jaynee R. Kim, Kenneth A. Hayes
Data type: species data
Explanation note: All material examined for *A. gagneorum* sp. nov. is provided in the body of the manuscript.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/zookeys.950.50669.suppl1