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Investigations

Tiny Snails With Large Distributions: Systematics and Delimitation of the Pacific Land Snails *Pacificella* and *Lamellidea* (Stylommatophora: Achatinellidae: Pacificellinae)

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Abstract

The Pacificellinae are a group of small, high-spired land snails distributed on islands across the Pacific. Some species are endemic to particular island groups, but others have wide geographic distributions, several of which have been attributed to anthropogenic transport between islands before western contact. We used DNA sequence data (COI, 16S, ITS2, 28S) from recently collected and historical specimens to estimate a phylogeny of the Pacificellinae, with a focus on Hawaiian species. Phylogenetic analyses support recognizing *Lamellidea* and *Pacificella* as distinct genera and indicate that the genus group *Tornatellinops* should be regarded as a synonym of *Lamellidea*. The number of taxa defined by species delimitation analyses (ASAP, bPTP, mPTP) varies widely, with between 6 and 42 species estimated in the Hawaiian Islands. These candidate species hypotheses were evaluated in an integrative framework, including shell morphology, geography, and a multilocus phylogeny, to revise the taxonomy of Hawaiian pacificellines. Four *Lamellidea* species and two Pacificella species are recognized from the Hawaiian Islands, including two widespread species introduced to Hawaiʻi from the South Pacific. *Lamellidea peponum* in Hawaiʻi shows little genetic divergence from Polynesian specimens previously referred to *L. oblonga*, and the name *L. oblonga* is now regarded as a junior synonym. *Lamellidea polygnampta* is recognized here from across the Hawaiian Islands, *L. cylindrica* from the island of Oʻahu, and the lowland species, *L. extincta*, from the main Hawaiian Islands and the Northwestern Islands. The only *Pacificella* specimens found in Hawaiʻi in modern surveys are more closely related to specimens of *P. variabilis* from Polynesia than to historical specimens of *P. baldwini*, indicating that the only *Pacificella* species now found in the main Hawaiian Islands appears to be introduced. Pacificellines have declined in abundance in Hawaiʻi over the last century and the two species *L. extincta* and *P. baldwini*, formerly present across the Hawaiian Islands, are now either critically endangered or extinct.

1 INTRODUCTION

The Hawaiian Islands are the most remote island chain in the world. Despite their isolation, representatives of 13 families of land snails have colonized the islands and diversified into more than 750 species, nearly all of which are endemic to the archipelago (Bouchet et al., 2017; Cowie et al., 1995; Mordan & Wade, 2008). The spectacularly colored and patterned shells of the larger (>5 mm) land snails in Hawaiʻi have long fascinated naturalists (Gulick, 1905; Newcomb, 1854; Swainson, 1828), but there are many lesser-known, smaller shelled species that have attracted far less research and conservation attention (Yeung & Hayes, 2018). As many as 60% of Pacific land snail genera comprise species with shells less than one centimeter in maximum width or height at adulthood (Vagvolgyi, 1975). The species-level diversity of these small land snails is not well understood, and many are highly endangered (Régnier et al., 2015; Yeung & Hayes, 2018). A variety of introduced species prey on Pacific Island land snails and have contributed to catastrophic declines in snail diversity and abundance. In Hawaiʻi, these include ants (e.g., *Pheidole* *megacephala*, Krushelnycky et al., 2005; Solem, 1990; Uchida et al., 2016), rats (*Rattus rattus*, *R. norvegicus*, and *R. exulans*, Hadfield et al., 1993; Hadfield & Saufler, 2008/2009; Solem, 1990), Jackson's chameleon (*Trioceros jacksonii xantholophus*, Chiaverano & Holland, 2014), the flatworm *Platydemus manokwari* (Gerlach et al., 2020; Sugiura & Yamaura, 2009), and the predatory snails *Euglandina* spp. (Gerlach et al., 2020; Hadfield et al., 1993; Meyer et al., 2016 and *Oxychilus alliarius* (Curry & Yeung, 2013; Meyer & Cowie, 2010). Ungulates and rats have also contributed indirectly to declines in land snail diversity and abundance through their impacts on native vegetation, which forms the foundation of the complex ecosystem on which snails rely (Meyer et al., 2014, 2021; Solem, 1990).

The Pacificellinae are a group of small, high-spired land snails in the family Achatinellidae that are distributed throughout Oceania and adjoining regions. The Achatinellidae is the second most diverse family of land snails in Hawaiʻi after the Amastridae (Cowie et al., 1995) and includes the highly threatened endemic achatinelline genera *Achatinella*, *Partulina*, *Perdicella*, and *Newcombia* (Gagne & Christensen, 1985; Solem, 1990; Yeung & Hayes, 2018), species of which are listed as endangered, critically endangered, extinct, or data deficient on the IUCN Red List (IUCN, 2021). Evolutionary relationships of the subfamily Achatinellinae have been investigated in several studies (Holland & Hadfield, 2004, 2007; M. R. Price et al., 2021; Thacker & Hadfield, 2000), and genomic diversity has been investigated in a few species following severe population bottlenecks (M. R. Price et al., 2015). Less is known about the systematics, ecology, biology, and conservation status of the smaller-shelled species in the subfamily Auriculellinae (Pilsbry & Cooke 1915 [in 1914–1916]; Cooke & Kondo, 1961; Yeung et al., 2020), and knowledge of microsnails (shell height < 5 mm, Liew et al., 2008) in the subfamilies Tornatellininae, Tornatellidinae, and Pacificellinae is poorer still (Pilsbry & Cooke 1915–1916 [in 1914–1916]; Cooke & Kondo, 1961).

The highest diversity of pacificelline species is in the Hawaiian Islands, where 10 species and three subspecies in two genera are currently recognized (Pilsbry & Cooke 1915 [in 1914–1916]; Cooke & Kondo, 1961). However, intraspecific variation in Hawaiian pacificellines is poorly understood, and it remains difficult to identify many individuals to species level. The Hawaiian Pacificellinae are minute, with shells between 2.0 and 4.5 mm in height at maturity. They occupy arboreal and epigeal habitats in forests from sea level to the highest peaks throughout the Hawaiian Islands. Previous studies indicated that all Hawaiian pacificellines except for *Lamellidea oblonga* (Pease, 1865) are endemic to the archipelago (Pilsbry & Cooke 1915 [in 1914–1916], pp. 162–164; Cooke & Kondo, 1961; Cowie, 1997). *Lamellidea oblonga* and two other pacificellines, *Lamellidea pusilla* (Gould, 1847) and *Pacificella variabilis* Odhner, 1922, have been interpreted as "canoe snails" that were likely transported between archipelagos of the Pacific by Polynesian voyagers. However, variation in shell morphology of specimens from across the Pacific makes it unclear whether these are single species or species complexes. These three pacificellines and two other achatinellids, *Tornatellides oblongus* (Tornatellidinae) and *Elasmias apertum* (Tornatellininae), have some of the widest geographic distributions known among Pacific Island land snails (Cooke & Kondo, 1961), but none to date have been assessed with molecular data in an integrative framework.

The classification of achatinellid microsnails at higher taxonomic levels has been established based on comparative anatomy, but, at the species level, most taxa have only been compared to closely related species using shell morphology (Cooke & Kondo, 1961). However, due to a scarcity of diagnostic morphological characters, species diversity in the Pacificellinae has remained poorly understood. To provide a framework for subsequent studies of their biology and a foundation from which to develop conservation priorities, the systematics of the Hawaiian Pacificellinae is examined for the first time using a multi-locus, molecular approach and includes DNA sequences from the type species of the genera *Lamellidea* and *Pacificella* from Hawaiʻi and of the genus *Tornatellinops* from the South Pacific. Mitochondrial DNA sequences are analyzed to delimit species and are considered in light of molecular phylogenies estimated from mitochondrial and nuclear DNA sequences. Intraspecific variation in shell morphology is illustrated using a combination of photographs, scanning electron microscopy, and micro-CT scans.

2 MATERIALS AND METHODS

2.1 Collection Data and Institutional Acronyms

The present study is based primarily on samples that were collected during field surveys carried out over the last fifteen years as part of ongoing efforts to document the remaining populations of native Hawaiian snails on all the main islands of Hawaiʻi. Pacificellines found in agricultural and horticultural facilities in Hawaiʻi are also included in our analyses (Table 1). Dried shells in the Bishop Museum collections from historical surveys between ~1890 and 1966 were also used to isolate DNA from unsampled taxa and locations of interest (Table 1).

Pacificellinae species were collected alive during surveys on all the main Hawaiian Islands between 2007 and 2019 and from New Zealand, Lord Howe Island (Australia), the Cook Islands, Tonga, and Niue between 2007 and 2017. Specimens from Hawaiʻi were killed in boiling water using the *niku-nuki* method (Fukuda et al., 2008) and then preserved in 95% ethanol. Specimens from elsewhere were killed by placing them into 95% ethanol. After tissue sampling, the remaining shells and bodies were transferred into 80% ethanol. Vouchers of all specimens collected for this study were deposited at the Bishop Museum (BPBM; Table 1). Additional ethanol-preserved samples were borrowed from the Australian Museum (AM), and DNA extracts were borrowed from the Smithsonian National Museum of Natural History (USNM). Specimens were identified to species based on morphological comparison to type material, original descriptions, and sequencing specimens from type lo-

Table 1. Specimen collection data with BOLD IDs for each individual, and the loci sequenced from each (COI, 16S, ITS2, and 28S).

Species	DNA #	COI hap. [# spm]	Voucher	Locality	agr/ hortic. site	Year	BOLD Process ID	COI	16S	ITS2	28S
L. peponum	PCMB54655	1 [40]	BPBM 288668	Hanalei, Kauaʻi, HI	x*	2013	ACHA106-22	√	√	√	√
	PCMB54656	5 [1]	BPBM 288670	Aitutaki, Cook Islands		2013	ACHA107-22	√			
	PCMB54657	2 [3]	BPBM 286943	Pāʻia, Maui, HI		2017	ACHA108-22	√	√	√	√
	PCMB54658	3 [1]	BPBM 287046	Kalāheo, Kauaʻi, HI	x	2015	ACHA109-22	√	√	√	√
	PCMB54659	4 [1]	BPBM 282784	Līhuʻe, Kauaʻi, HI		2007	ACHA110-22	√	√		
	USNM1425068	6 [1]	USNM 1425068	Moʻorea, French Polynesia		2010	ACHA111-22	√	√	√	√
	USNM1425073	7 [2]	USNM 1425073	Moʻorea, French Polynesia		2010	ACHA112-22	√	√	√	
L. cylindrica	PCMB54645	8 [1]	BPBM 270663	Kahuku, Oʻahu, HI		2007	ACHA113-22	√	√		√
	PCMB54646	9 [1]	BPBM 288662	Lualualei, Oʻahu, HI		2012	ACHA114-22	√			√
	PCMB54647	10 [1]	BPBM 288704	Mokulēʻia, Oʻahu, HI		2018	ACHA115-22	√	√	√	√
	PCMB54648	11 [2]	BPBM 288696	Palawai, Oʻahu, HI		2018	ACHA116-22	√	√		√
	PCMB54649	12 [1]	BPBM 288706	Makiki, Oʻahu, HI		2019	ACHA117-22	√	√	√	√
	PCMB54650	13 [2]	BPBM 288706	Makiki, Oʻahu, HI		2019	ACHA118-22	√	√		√
	PCMB54651	14 [3]	BPBM 288709	Kuliouou, Oʻahu, HI		2000s	ACHA119-22	√	√	√	√
	PCMB54652	15 [1]	BPBM 270663	Kahuku, Oʻahu, HI		2007	ACHA120-22	√			
	PCMB54653	16 [1]	BPBM 288710	Wiliwilnui, Oʻahu, HI		2000s	ACHA121-22	√			
	PCMB54654	17 [1]	BPBM 288711	Wiliwilnui, Oʻahu, HI		2000s	ACHA122-22	√			
	PCMB50677	18 [2]	BPBM 182809	Waiʻanae, Oʻahu, HI		~1939	ACHA123-22	√			
L. extincta	PCMB50628	[2]	BPBM 188760	Lualualei, Oʻahu, HI		~1939	ACHA126-22	√			
	PCMB50481	[1]	BPBM 13645	Laysan		~1911	ACHA124-22	√			
	PCMB50482	[1]	BPBM 13645	Laysan		~1911	ACHA125-22	√			

Species	DNA #	COI hap. [# spm]	Voucher	Locality	agr/ hortic. site	Year	BOLD Process ID	COI	16S	ITS2	28S
	PCMB51683	[1]	BPBM 189607	Wake Island		~1941	ACHA127-22	√			
L. polygnampta	PCMB54610	25 [1]	BPBM 288664	Kamakou, Molokaʻi, HI		2012	ACHA128-22	√	√	√	√
	PCMB54611	44 [1]	BPBM 288665	Hanalei, Kauaʻi, HI		2012	ACHA129-22	√	√	√	√
	PCMB54612	36 [1]	BPBM 288673	Wahiawa, Oʻahu, HI		2013	ACHA130-22	√	√	√	√
	PCMB54613	19 [1]	BPBM 288672	Waimea, Hawaiʻi, HI		2013	ACHA131-22	√	√	√	
	PCMB54614	20 [1]	BPBM 288671	Waimea, Hawaiʻi, HI		2013	ACHA132-22	√	√	√	√
	PCMB54615	37 [1]	BPBM 288677	Palikea, Oʻahu, HI		2014	ACHA133-22	√	√	√	√
	PCMB54616	28 [1]	BPBM 288678	Kapalua, Maui, HI		2014	ACHA134-22	√	√		
	PCMB54617	22 [1]	BPBM 288681	Olowalu, Maui, HI		2015	ACHA135-22	√	√	√	√
	PCMB54618	41 [1]	BPBM 288682	Nakula NARS, Maui, HI		2015	ACHA136-22	√	√		
	PCMB54619	33 [5]	BPBM 288683	Waiākea Forest Reserve, Hawaiʻi, HI		2015	ACHA137-22	√	√		
	PCMB54620	23 [1]	BPBM 288697	Palawai, Oʻahu, HI		2018	ACHA138-22	√	√	√	√
	PCMB54621	23 [1]	BPBM 288697	Palawai, Oʻahu, HI		2018	ACHA139-22	√	√		
	PCMB54622	39 [1]	BPBM 288695	Olokui NARS, Molokaʻi, HI		2018	ACHA140-22	√	√		
	PCMB54623	47 [1]	BPBM 288700	Palawai, Oʻahu, HI		2018	ACHA141-22	√	√	√	√
	PCMB54624	43 [1]	BPBM 288699	Palawai, Oʻahu, HI		2018	ACHA142-22	√			
	PCMB54625	38 [1]	BPBM 288694	Hāna, Maui, HI		2017	ACHA143-22	√	√	x2	√
	PCMB54626	50 [1]	BPBM 288700	Palawai, Oʻahu, HI		2018	ACHA144-22	√			
	PCMB54627	48 [2]	BPBM 288700	Palawai, Oʻahu, HI		2018	ACHA145-22	√	√	√	√
	PCMB54628	40 [4]	BPBM 288698	Palawai, Oʻahu, HI		2018	ACHA146-22	√	√	x2	√
	PCMB54629	42 [1]	BPBM 288703	Mokulēʻia, Oʻahu, HI		2018	ACHA147-22	√	√	√	√
	PCMB54630	46 [1]	BPBM 288702	Nuʻuanu, Oʻahu, HI		2018	ACHA148-22	√	√	√	√

Species	DNA #	COI hap. [# spm]	Voucher	Locality	agr/ hortic. site	Year	BOLD Process ID	COI	16S	ITS2	28S
	PCMB54631	24 [1]	BPBM 288701	Nuʻuanu, Oʻahu, HI		2018	ACHA149-22	√	√	√	√
	PCMB54632	33 [5]	BPBM 288705	Waiʻanae, Oʻahu, HI		2018	ACHA150-22	√			
	PCMB54633	44 [2]	BPBM 288690	Puʻu Hapapa, Oʻahu, HI		2017	ACHA151-22	√	√	√	√
	PCMB54634	35 [1]	BPBM 288688	Puʻu Hapapa, Oʻahu, HI		2017	ACHA152-22	√	√		√
	PCMB54635	52 [1]	BPBM 288691	Puʻu Hapapa, Oʻahu, HI		2017	ACHA153-22	√	√	√	√
	PCMB54636	26 [1]	BPBM 288689	Puʻu Hapapa, Oʻahu, HI		2017	ACHA154-22	√	√		
	PCMB54637	21 [1]	BPBM 288685	Makawao, Maui, HI		2016	ACHA155-22	√	√		
	PCMB54638	49 [1]	BPBM 288684	Pearl City, Oʻahu, HI		2015	ACHA156-22	√	√	√	√
	PCMB54639	45 [1]	BPBM 288684	Pearl City, Oʻahu, HI		2015	ACHA157-22	√	√	√	√
	PCMB54640	42 [1]	BPBM 288699	Palawai, Oʻahu, HI		2018	ACHA158-22	√	√	√	√
	PCMB54641	51 [1]	BPBM 288686	Makawao, Maui, HI		2016	ACHA160-22	√			
	PCMB54642	34 [1]	BPBM 288667	Puʻu Hapapa, Oʻahu, HI		2013	ACHA161-22	√	√		
	PCMB54643	30 [1]	BPBM 288663	Nuʻalolo, Kauaʻi, HI		2012	ACHA162-22	√	√		
	PCMB54644	31 [1]	BPBM 288651	Lanaʻi City, Lanaʻi, HI		2008	ACHA163-22	√	√		√
	PCMB56229	NA [2]	BPBM 289091	Puʻu Hapapa, Oʻahu, HI		2013	n/a (see ACHA153-22)	√			
	PCMB56230	45 [1]	BPBM 288716	Nuʻuanu, Oʻahu, HI		2018	ACHA164-22	√			
	PCMB50616	NA [1]	BPBM 18673	Hawaiʻi, HI		~1911	ACHA165-22	√			
	PCMB50680	27 [2]	BPBM 170414	Makawao, Maui, HI		~1912	ACHA166-22	√			
	PCMB50681	29 [1]	BPBM 170414	Makawao, Maui, HI		~1912	ACHA167-22	√			
	PCMB50683	32 [1]	BPBM 109670	East Maui, Maui, HI		~1912	ACHA168-22	√			

Species	DNA #	COI hap. [# spm]	Voucher	Locality	agr/ hortic. site	Year	BOLD Process ID	COI	16S	ITS2	28S
	PCMB50685	NA [1]	BPBM 24290	Puʻu kolekole, Molokaʻi, HI		~1912	ACHA169-22	√			
Lamellidea sp.	PCMB54664	[1]	BPBM 288656	Alofi, Niue		2010	ACHA192-22	√			√
L. lidgbirdensis	PCMB52011	[1]	AM C.574969	Lord Howe Island, Australia		2019	ACHA170-22	√			√
L. micropleura	USNM1425107	[1]	USNM 1425107	Moʻorea, French Polynesia		2010	ACHA171-22	√	√		√
	USNM1425108	[2]	USNM 1425108	Moʻorea, French Polynesia		2010	ACHA172-22	√	√		
	USNM1425109	[1]	USNM 1425109	Moʻorea, French Polynesia		2010	ACHA173-22	√			
L. novoseelandica	PCMB54665	[1]	BPBM 288661	Northland, North Island, New Zealand		2011	ACHA174-22	√		√	
	PCMB54666	[1]	BPBM 288661	Northland, North Island, New Zealand		2011	ACHA175-22	√		√	
	PCMB54667	[1]	BPBM 288658	Lord Howe Island, Australia		2010	ACHA176-22	√			
	PCMB54668	[1]	BPBM 288655	Three Kings Island, New Zealand		2008	ACHA177-22	√			
	PCMB54669	[2]	BPBM 288680	Nelson, South Island, New Zealand		2014	ACHA181-22	√	√		√
	PCMB54670	[1]	BPBM 288659	Chatham Island, New Zealand		2011	ACHA182-22	√			
	PCMB51686	[1]	AM C.392221	Lord Howe Island, Australia		2000	ACHA178-22	√			
	PCMB51689	[1]	AM C.559477	New South Wales, Australia		2017	ACHA179-22	√			
	PCMB51690	[1]	AM C.574950	Lord Howe Island, Australia		2019	ACHA180-22	√	√		√
	PCMB52010	[1]	AM C.395538.001	Norfolk Island, Australia		1999	ACHA183-22	√			
L.	PCMB54660	[1]	BPBM 288652	Ogasawara, Japan		2006	ACHA184-22	√	√	√	√

Species	DNA #	COI hap. [# spm]	Voucher	Locality	agr/ hortic. site	Year	BOLD Process ID	COI	16S	ITS2	28S
ogasawarana											
	PCMB54661	[1]	BPBM 288653	Ogasawara, Japan		2006	ACHA185-22	√	√		
L. pusilla	PCMB54662	[1]	BPBM 288676	Maninita, Vava‘u, Tonga		2014	ACHA186-22	√	√		√
	PCMB54663	[1]	BPBM 288693	Alofi, Niue		2017	ACHA187-22	√	√	√	√
	PCMB50687	[1]	BPBM 3353	Society Islands		~1890	ACHA189-22	√			
	PCMB50693	[2]	BPBM 212720	Saipan, Marianas		~1949	ACHA190-22	√			
	PCMB50674	[1]	BPBM 288712	Solomon Islands		~1966	ACHA188-22	√	√		√
	PCMB50691	[2]	BPBM 213592	Tinian, Marianas		~1952	ACHA191-22	√			
P. baldwini	PCMB50626	[2]	BPBM 25081	Hilo, Hawai‘i, HI		~1913	ACHA194-22	√			
	PCMB50488	[1]	BPBM 18610	Kaupakalua, Maui, HI		~1906	ACHA193-22	√			
	PCMB50478	[2]	BPBM 288713	Kure Atoll		~1961	ACHA195-22	√			
	PCMB51680	[3]	BPBM 57540	Johnston Atoll		~1923	ACHA196-22	√			√
P. variabilis	PCMB50490	[2]	BPBM 288708	Tahiti, French Polynesia		2019	ACHA198-22	√			
	PCMB50670	[2]	BPBM 207570	Easter Island		~1965	ACHA211-22	√			
	PCMB50675	[1]	BPBM 288714	Solomon Islands		~1966	ACHA212-22	√			√
	PCMB51688	[1]	AM C.487474	Vanuatu		2014	ACHA213-22	√			
	PCMB54671	[1]	BPBM 288675	Schofield, O‘ahu, HI		2013	ACHA197-22	√			
	PCMB54672	[2]	BPBM 286835	Kilauea, Kaua‘i, HI	x	2017	ACHA200-22	√	√		√
	PCMB54673	[7]	BPBM 288707	Makiki, O‘ahu, HI		2019	ACHA201-22	√	√	√	√
	PCMB54674	[1]	BPBM 288654	Mangaia, Cook Islands		2007	ACHA202-22	√			
	PCMB54675	[1]	BPBM 288669	Aitutaki, Cook Islands		2013	ACHA203-22	√	√		√
	PCMB54676	[1]	BPBM 288657	Alofi, Niue		2010	ACHA204-22	√			
	PCMB54677	[3]	BPBM 288674	Tinian, Mariana Islands		2013	ACHA205-22	√	√		√

Species	DNA #	COI hap. [# spm]	Voucher	Locality	agr/ hortic. site	Year	BOLD Process ID	COI	16S	ITS2	28S
	PCMB54678	[1]	BPBM 288660	Saipan, Mariana Islands		2011	ACHA206-22	√	√	√	√
	PCMB54679	[1]	BPBM 288679	Tiapa Valley, Tahiti, French Polynesia		2014	ACHA199-22	√	√	√	√
	USNM1425133	[1]	USNM 1425133	Mo‘orea, French Polynesia		2010	ACHA207-22	√			
	USNM1425104	[3]	USNM 1425104	Mo‘orea, French Polynesia		2010	ACHA208-22	√	√	√	√
	USNM1425135	[1]	USNM 1425135	Mo‘orea, French Polynesia		2010	ACHA209-22	√			
	USNM1425077	[2]	USNM 1425077	Mo‘orea, French Polynesia		2010	ACHA210-22	√	√	√	√
Elasmias apertum	PCMB54680		BPBM 288692	Alofi, Niue		2017	ACHA215-22	√	√		√
Fernandezia sp.	PCMB54682		BPBM 288666	Juan Fernandez		2012	ACHA214-22	√	√		
Tornatellides subperforata	PCMB54681		BPBM 288687	Auckland, New Zealand		2016	ACHA216-22	√	√	√	√

COI haplotype number is an identifier used to identify unique haplotypes in haplotype maps (Fig. 3). NA denotes short COI sequences not included in the haplotype maps. The number in brackets indicates the number of specimens that share that COI haplotype. Specimens collected from agricultural or horticultural sites are noted (* indicates a particular voucher was found at a natural site, but other individuals with the same COI haplotype were found in agricultural or horticultural facilities). A check mark in the column for COI, 16S, ITS2 or 28S indicates that the specimen was sequenced for that locus. Individuals with two ITS2 haplotypes, separated by phasing, are indicated with “x2” in the ITS2 column. GPS coordinates for native Hawaiian snails collected during the last 20 years are not provided here for conservation purposes but are kept in the State of Hawai‘i Department of Land and Natural Resources Snail Extinction Prevention Program and Bishop Museum Malacology databases and are available upon request.

calities when possible. One undescribed species represented by only a single sequenced specimen is left in open nomenclature until additional specimens can be collected.

Type material was examined from the Australian Museum, Sydney, New South Wales, Australia (AM); Academy of Natural Sciences, Drexel University, Philadelphia, Pennsylvania, USA (ANSP); Bernice Pauahi Bishop Museum, Honolulu, Hawaiʻi, USA (BPBM); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Natural History Museum, London, United Kingdom (NHMUK); Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS); Swedish Museum of Natural History, Stockholm, Sweden (SMNH); and the Smithsonian Institution, National Museum of Natural History, Washington, D.C., USA (USNM). Lectotypes are designated for two Hawaiian species to clarify the application of available species-group names.

2.2 Microscopy

Radulae were examined from selected ethanol-preserved specimens of *Lamellidea* and *Pacificella* species from Hawaiʻi. The buccal mass was digested in 180 µL of T1 lysis buffer (Macherey-Nagel) containing 20 mg/mL of Proteinase-K. Following tissue digestion, radulae were rinsed in de-ionized water. Cleaned radulae were mounted on adhesive tabs attached to aluminum stubs and coated with 25–30 nm gold/palladium (60/40). Shells of selected specimens were also mounted on aluminum stubs and stabilized with Elmer's glue. After drying completely, the shells were coated to image the protoconch. Radulae and shells were imaged using an Apreo scanning electron microscope (FEI Company) at the National Museum of Natural History, Washington.

Shells were photographed with a ruler for scale on a Leica M125 stereo microscope with an attached Canon EOS T5i digital camera. Shell height was measured using ImageJ software (Rueden et al., 2017). Selected specimens were micro-CT scanned with the GE Phoenix v|tome|x M 180kV Nano Tube at the Smithsonian National Museum of Natural History Scientific Imaging Facility. Volume files for the shells were made with Amira 2019.3 by Thermo Fisher Scientific. Shell images and 3D micro-CT models were uploaded to the online database MorphoBank, http://morphobank.org/permalink/?P565.

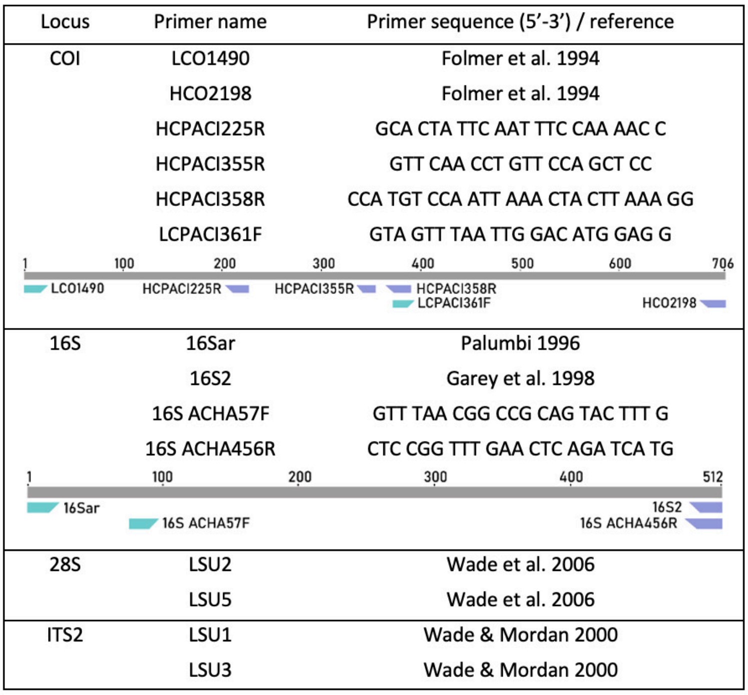
2.3 DNA isolation and PCR amplification

A small piece of tissue (ca. 0.5 mm^3) was removed from the foot of ethanol preserved specimens with sterile forceps for DNA isolation. Total genomic DNA (gDNA) was extracted from 260 Pacificellinae specimens and 3 achatinellid outgroups. In addition, an aliquot of gDNA was provided by USNM for 15 specimens from French Polynesia. The gDNA was isolated from recently collected specimens using the Nucleospin DNA tissue kit following the manufacturer's protocol (Machery Nagel, PA, USA), with an overnight incubation and a total elution of 60 µl. Historical specimens with dried tissue inside the shell were extracted whole using the E.Z.N.A. Mollusc DNA Kit (Omega Bio-Tek) with a three-day incubation (Goulding et al., 2021). For each set of samples, a negative control with all reagents underwent the same extraction process to test for the presence of exogenous DNA contamination. A fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified and sequenced from 193 specimens: 133 individuals from the main Hawaiian Islands and 60 individuals from other Pacific Islands, New Zealand, and Australia. Of these, 163 samples were preserved in ethanol and 30 were dried museum specimens collected before 1966. For Hawaiian species, the mitochondrial 16S rRNA gene was amplified from one individual per COI haplotype. For non-Hawaiian species, two to three specimens per species were selected for 16S amplification. The nuclear ribosomal internal transcribed spacer ITS2 was amplified along with part of the ribosomal 5.8S and 28S region from 40 *Lamellidea* and 2 *Pacificella* specimens from Hawaiʻi, as well as 8 *Lamellidea* and 4 *Pacificella* from outside Hawaiʻi (New Zealand, French Polynesia, Cook Islands, Niue, Mariana Islands, and Japan). For each species, one specimen was selected for amplification of 28S, with additional specimens sequenced from Hawaiian *Lamellidea* species and species with high intraspecific diversity (*L. novoseelandica*, *L. pusilla*, and *P. variabilis*). Negative PCR controls consisting of sterile water instead of DNA template were used to test for contamination.

Amplifications for all loci were carried out in 25 µl PCR reactions with a final concentration of 1X MangoTaq Buffer (Bioline, Tauntan, MA, USA), 2.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.14-0.16 µM of each primer (Table 2), 0.4 µg/µl BSA, 0.5% DMSO, 1 U MangoTaq Polymerase (Bioline, Tauntan, MA, USA), and 1–2 µl template DNA. Cycling parameters for COI consisted of an initiation cycle of 5 minutes at 95 °C, 1 minute at 44 °C, and 1 minute at 72 °C; followed by 34 cycles of 1 minute at 95 °C, 40 seconds at 46 °C, and 50 seconds at 72 °C; and a 3 minute final extension at 72 °C. Amplification of 16S differed in that the annealing temperature was raised to 48 °C for the initial cycle and, the subsequent 34 cycles were 30 seconds at 95 °C, 20 seconds at 50 °C, and 25 seconds at 72 °C; the final extension remained the same. The thermocycling parameters for ITS2 followed the protocol of Wade and Mordan (2000). Cycling parameters for 28S differed from COI in that the annealing temperature of the initial cycle was 47 °C; followed by 34 cycles of 30 seconds at 95 °C, 20 seconds at 49 °C, and 45 seconds at 72 °C; and the final extension at 72° C was 5 minutes. PCR products were sent to Eurofins Scientific (Louisville, KY, USA) for PCR cleanup and Sanger sequencing on an ABI 3730XL.

2.4 Phylogenetic analyses

Chromatograms were checked for errors and edited in Geneious v. 9.1.8 (Kearse et al., 2012) after assembling forward and reverse sequences into contigs. Consensus sequences were then extracted for each sample and aligned using MUSCLE (Edgar, 2004) as implemented in Geneious. Heterozygous sequences of ITS2 were phased using Champuru (Flot, 2007). In some cases, the presence of more than



Locus	Primer name	Primer sequence (5'-3') / reference
COI	LCO1490	Folmer et al. 1994
	HCO2198	Folmer et al. 1994
	HCPACI225R	GCA CTA TTC AAT TTC CAA AAC C
	HCPACI355R	GTT CAA CCT GTT CCA GCT CC
	HCPACI358R	CCA TGT CCA ATT AAA CTA CTT AAA GG
	LCPACI361F	GTA GTT TAA TTG GAC ATG GAG G
16S	16Sar	Palumbi 1996
	16S2	Garey et al. 1998
	16S ACHA57F	GTT TAA CGG CCG CAG TAC TTT G
	16S ACHA456R	CTC CGG TTT GAA CTC AGA TCA TG
28S	LSU2	Wade et al. 2006
	LSU5	Wade et al. 2006
ITS2	LSU1	Wade & Mordan 2000
	LSU3	Wade & Mordan 2000

Table 2. Names and sequences for primers used in this study or the reference for previously published primers. The positions of new COI and 16S primers are indicated with respect to an alignment of pacificelline sequences.

two length variant ITS2 haplotypes in an individual could not be resolved by phasing, and the ITS2 sequences could not be used. Three non-pacificelline achatinellid species (*Tornatellides subperforata*, *Elasmias apertum*, and *Fernandezia* sp.) were used as outgroups. All unique DNA haplotypes were deposited in the Barcode of Life Database, BOLD (Table 1). The lengths of the alignments analyzed were 654 bp for COI, 472 bp for 16S, 934 bp for 5.8S-ITS2-28S, and 546 bp for 28S.

Gblocks 0.91b (Talavera & Castresana, 2007) was used to remove ambiguously aligned regions from the 16S alignment, and both the full and the Gblocks alignments were used in phylogenetic analyses to evaluate any differences created by removing such regions. The 16S alignment after trimming with Gblocks was 409 bp. Maximum likelihood analysis was performed with IQ-TREE (Chernomor et al., 2016; Minh et al., 2020; Nguyen et al., 2014/2015) using the integrated ModelFinder function (Kalyaanamoorthy et al., 2017). Analyses were done on a partitioned COI alignment: the first analysis was done with each codon partitioned separately, and a second analysis was done with the first and second codon positions partitioned separately from the third codon position. Bayesian Information Criterion (BIC) scores were compared between the two analyses. The best BIC score estimated by ModelFinder in IQ-Tree was for partitioning the first and second codon positions of COI together as a separate partition from the third codon position. For the maximum likelihood analysis, the best nucleotide models for these partitions were TIM+F+ G4 for the first and second codon positions and GTR+F+G4 for the third position. A concatenated alignment of COI, 16S, ITS2, and 28S was made with the 1st and 2nd codon positions of COI partitioned separately from the third codon and the other loci (i.e., 5 partitions). In the multilocus alignment, the models for COI codons are the same as above, and TPM2u + F +I + G4 was used for 16S, TPM3u + F + G4 for ITS2, and TIM2 + F + G4 for 28S. Clade reliability support was estimated with 1,000 ultra-fast bootstrap replicates. Indels in nuclear ITS2 sequences were coded using FastGap v. 1.2 (Borchsenius, 2009) using simple indel coding (Simmons & Ochoterena, 2000) to distinguish closely related species in the maximum likelihood analysis. Two partitions were used in estimating this IQ-Tree analysis, one with the ITS2 sequence including the adjacent partial 5.8 and 28S sequences and a second with the indel coding. A second analysis was conducted with four partitions: the 5.8S, ITS2, and 28S regions partitioned separately in IQ Tree from the indel coding. The K2P+G4 model was used for the ITS2 sequences, and the F81+F+ASC was used for the indel coding. For Bayesian analyses of the multilocus dataset, the best-fit model of nucleotide substitution identified by IQ-Tree was used as the basis for the partitioning scheme for MrBayes. The best-fit models for each partition were GTR + G + I (COI 1st and 2nd codons as one partition, 16S partitioned separately) and GTR + G (COI 3rd codon, ITS and 28S each partitioned separately). Bayesian analyses of partitioned data were performed using MrBayes v. 3.2.7 (Ronquist et al., 2012) on the CIPRES Science Gateway (Miller et al., 2010). Each MrBayes run consisted of two simultaneous runs with 4 chains of 5 x 10^6 generations each, a sampling frequency of 500, and a burn-in of 25%. Nodal support was assessed with posterior probabilities. Effective sampling size and convergence diagnostics were reviewed at the end of each run.

2.5 Species delimitation and haplotype networks

Uncorrected pairwise distances were calculated in MEGA 7 (Kumar et al., 2016), assuming uniform rates among sites. Species delimitation follows phylogenetic criteria under the Unified Species Concept (De Queiroz, 2007). Three methods were used to delineate species based on mitochondrial COI sequences without *a priori* group designations: Assemble Species by Automatic Partitioning, or ASAP, (Puillandre et al., 2021) using the Jukes-Cantor (JC69) substitution model, bPTP (Zhang et al., 2013), and mPTP (Kapli et al., 2017). The input for the bPTP and mPTP analyses was a maximum likelihood tree estimated based on COI sequences in IQ-Tree.

Median-joining haplotype networks were constructed for Hawaiian *Lamellidea* species based on COI sequences in POPART v. 1.7 (Leigh & Bryant, 2015). Approximately 335 bp of the 5' region of the COI alignments were used for haplotype analyses to allow the inclusion of short sequences from historical samples. The lengths of the alignments used were 337 bp for *Lamellidea peponum*, 336 bp for *L. cylindrica*, and 363 bp for other Hawaiian *Lamellidea* species.

2.6 Geographic and elevational distributions

The localities of the specimens analyzed in this study were plotted on a map of Hawai‘i using QGIS v3.8.2 (QGIS, 2019). A box and whisker plot was used to illustrate the elevational ranges of pacificelline species present in Hawai‘i, with the exception of *P. baldwini*. Specimens of *P. baldwini* used in DNA analyses did not include elevation data or precise localities that could be used to estimate elevation. A Tukey HSD test was conducted in Microsoft Excel 365 to test differences among the mean elevations of the species for significance. Only species with elevation records for three or more localities were included.

3 RESULTS

3.1 Phylogenetic relationships and species delimitation

The phylogenetic tree estimated by COI sequences produced a phylogeny with two genetically divergent clades that are highly supported, which correspond to the genera *Lamellidea* and *Pacificella* (bootstrap support or BS 100, Fig. 1a). The number of species defined by delimitation analyses varied widely. Multiple delimitations of species are possible with ASAP, and multiple highly scored partitions should be considered (Puillandre et al., 2021). The highest scoring partition in ASAP suggested 97 species, the second-highest partition indicated 60 species, and the lowest number of species delimited was 39, a scenario that ranked ninth out of the top ten highest scores. The delimitation of 97 species is seven times higher than the delimitation with mPTP and is higher than expected based on the known diversity of other land snails in Hawai‘i; so, we instead compared the 2nd highest ranked partition with 60 species (ASAP #2, Fig. 1a) and the more conservative delimitation of 39 species (ASAP #9, Fig. 1a). In bPTP, 23 species were delimited, compared to 13 species with mPTP (Fig. 1). Average support values in the mPTP analysis for nodes between species were all greater than 0.985. Bayesian support values for the species delimited with bPTP are reported in Fig. 1a. Several of the species delimited by ASAP are paraphyletic in the COI gene tree: three of the species delimited by ASAP #2 [part of *L. cylindrica* (1), *L. polygnampta* (2), and *L. pusilla* (3)] and two of the species delimited by ASAP #9 [part of *L. cylindrica* (1), *L. polygnampta* (2)] (Fig. 1a). The mPTP species delimitation analysis was the best supported by the analysis of nuclear ITS2 data (Fig. 1b).

The full alignments of the 16S locus were used for the analyses of the concatenated dataset presented here, which produced a tree with two clades—both with nearly full support (BS 99–100, PP 1, Fig. 2). Phylogenetic trees based on alignments modified by Gblocks recovered the same phylogenetic relationships between species as the full alignments (Supp. Figs. 1-2). Bayesian and maximum likelihood analyses of the multilocus dataset recovered a tree similar in topology to that estimated from the mitochondrial data alone. However, the relationships of *Lamellidea pusilla*, *Lamellidea* sp. (Niue), and the clade including *L. peponum*, *L. micropluera*, and *L. ogasawarana* to other *Lamellidea* species all have low support (Fig. 2).

Two genetically divergent clades are identified in *Pacificella*, one of which includes specimens from Hawai‘i, Johnston Atoll, Kure, and Maui that we attribute to *Pacificella baldwini* (Figs. 1a, 2). The specimens from Kure and Johnston were identified as a distinct species in the ASAP #2 and bPTP analyses, but not by ASAP #9 or mPTP (Fig. 1a). A second clade is comprised of specimens from Kaua‘i, O‘ahu, and islands in Micronesia, Melanesia, and southern Polynesia that we attribute to *Pacificella variabilis*. The individuals in this clade were considered to represent either a single species (mPTP) or between 5 species (bPTP) and 10 species (ASAP #2). Genetic divergence between the *P. baldwini* and *P. variabilis* clades is 3.8–8.8% in COI. *Pacificella baldwini* was highly supported in the analysis of COI sequences (BS 95, Fig. 1a) and the multilocus analyses (BS 97), while *P. variabilis* had slightly lower support (BS 94, Fig. 1a; BS 92, Fig. 2).

Our analyses identified several clades within *Lamellidea* (Figs. 1a, 2). One of these includes a topotypic representative of the type species of *Tornatellinops* Pilsbry & Cooke, 1915. We recognize ten species in the *Lamellidea* clade, as shown in Fig. 2 and outlined in the systematic section below: *Lamellidea peponum*, *L. cylindrica*, *L. extincta, L. polygnampta* in Hawai‘i; *T. novoseelandica* in Australia, New Zealand, Lord Howe Island, and Norfolk Island; *T. lidgbirdensis* in Lord Howe Island; *L. pusilla* in Micronesia, Melanesia, and southern Polynesia; *L. micropleura* and *Lamellidea* sp. in southern Polynesia; and *L. ogasawarana* in Japan. All the *Lamellidea* species that are represented in the analysis by more than one specimen have high support in multilocus phylogenetic analyses (BS > 95 and PP > 0.95, except for *L. polygnampta*, BS 90, PP 0.95).

Specimens of Hawaiian *Lamellidea* that had been identified morphologically as *L. polygnampta, L. polygnampta*

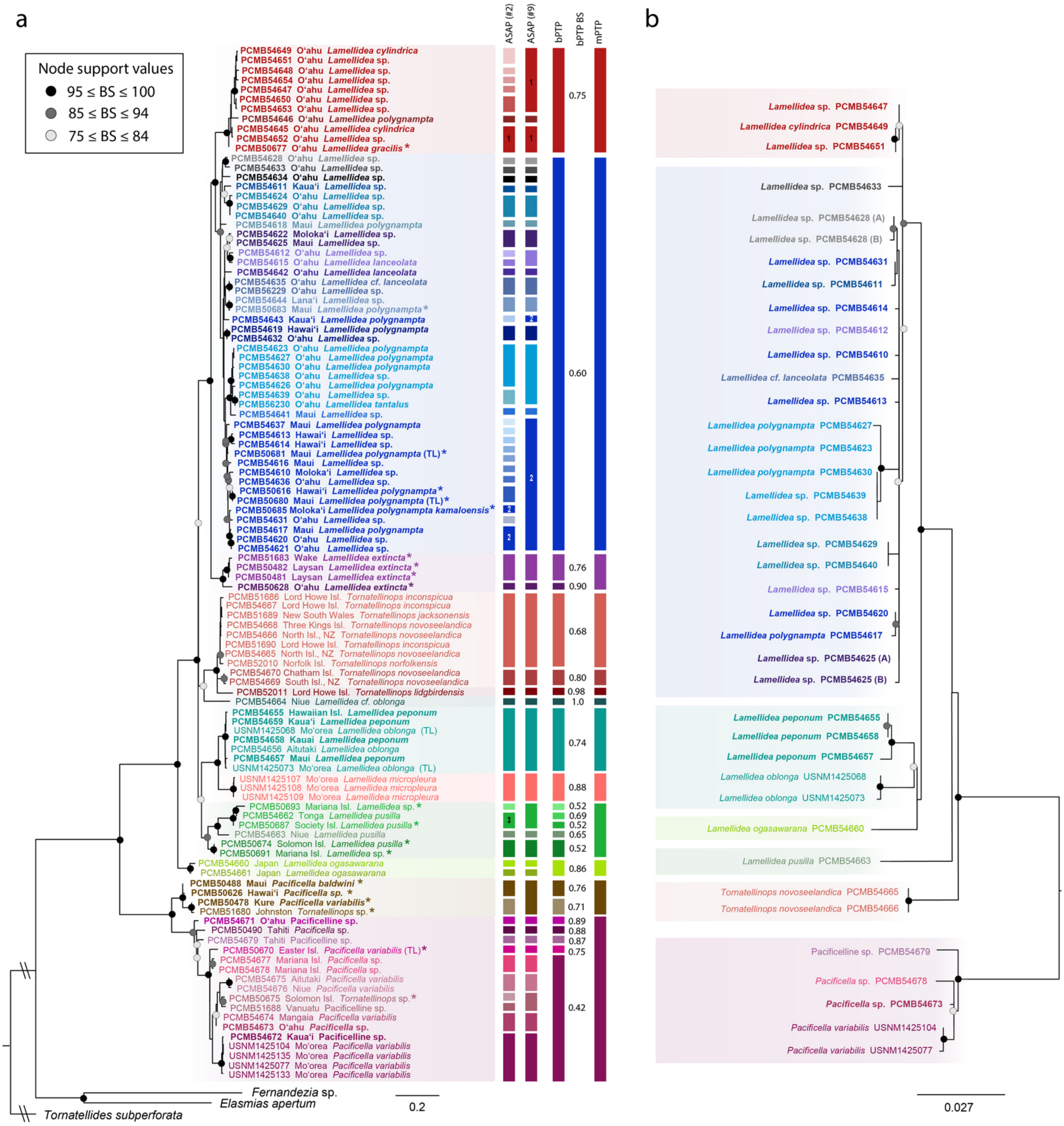


Figure 1. Phylogenetic trees with bootstrap support values indicated by shaded circles at the nodes.

(a) Maximum likelihood phylogenetic tree based on partitioned analysis of COI sequences estimated with IQ-Tree with localities and original morphological identifications of specimens. Specimens from the Hawaiian Islands are in bold. TL indicates specimens sequenced from the type locality of that species, and * marks historical specimens (collected in the 1960s or earlier). Species delimitation analyses of COI sequences using ASAP (the partitions with the 2nd highest and 9th highest scores), bPTP, and mPTP are illustrated by the colored blocks to the right of the tree. Specimens in the tree are colored according to the partitions from ASAP #9. Groups identified in species delimitation analyses that are not monophyletic in the phylogenetic tree are identified with numbers inside the delimitation blocks (three groups in ASAP # 2 are paraphyletic, and two groups in ASAP #9). (b) Maximum likelihood tree based on sequences of partial 5.8S-ITS2-28S. Haplotypes from heterozygous individuals are indicated with "A" or "B" after the specimen registration number.

kamaloensis, *L. cylindrica, L. lanceolata, L. tantalus,* and *L. extincta* form a well-supported clade in the mitochondrial (Fig. 1a), multilocus (Fig. 2, BS 99, PP 1), and ITS2 (BS 87, Fig. 1b) analyses, albeit in the latter with reduced taxonomic sampling. *Lamellidea extincta*, present on both the Northwestern Hawaiian Islands (or Leeward Islands) and the main Hawaiian Islands, is sister group to a clade including *Lamellidea cylindrica*, which is known only from Oʻahu, and *Lamellidea polygnampta* (BS 99, PP 1). Intraspecific uncorrected pairwise distances in COI sequences are up to 7.9% in Hawaiian *Lamellidea* species, while interspecific divergence as low as 4.3% was observed between *L. peponum* and *L. micropleura*, indicating substantial overlap between intra- and interspecific diversity (Table S1).

Phylogenetic analyses place *L. peponum* as sister to *L. micropleura* from French Polynesia (BS 100, PP 1). *Lamellidea peponum* belongs to a well-supported clade that includes *L. oblonga* from Aitutaki, Cook Islands, and Moʻorea,

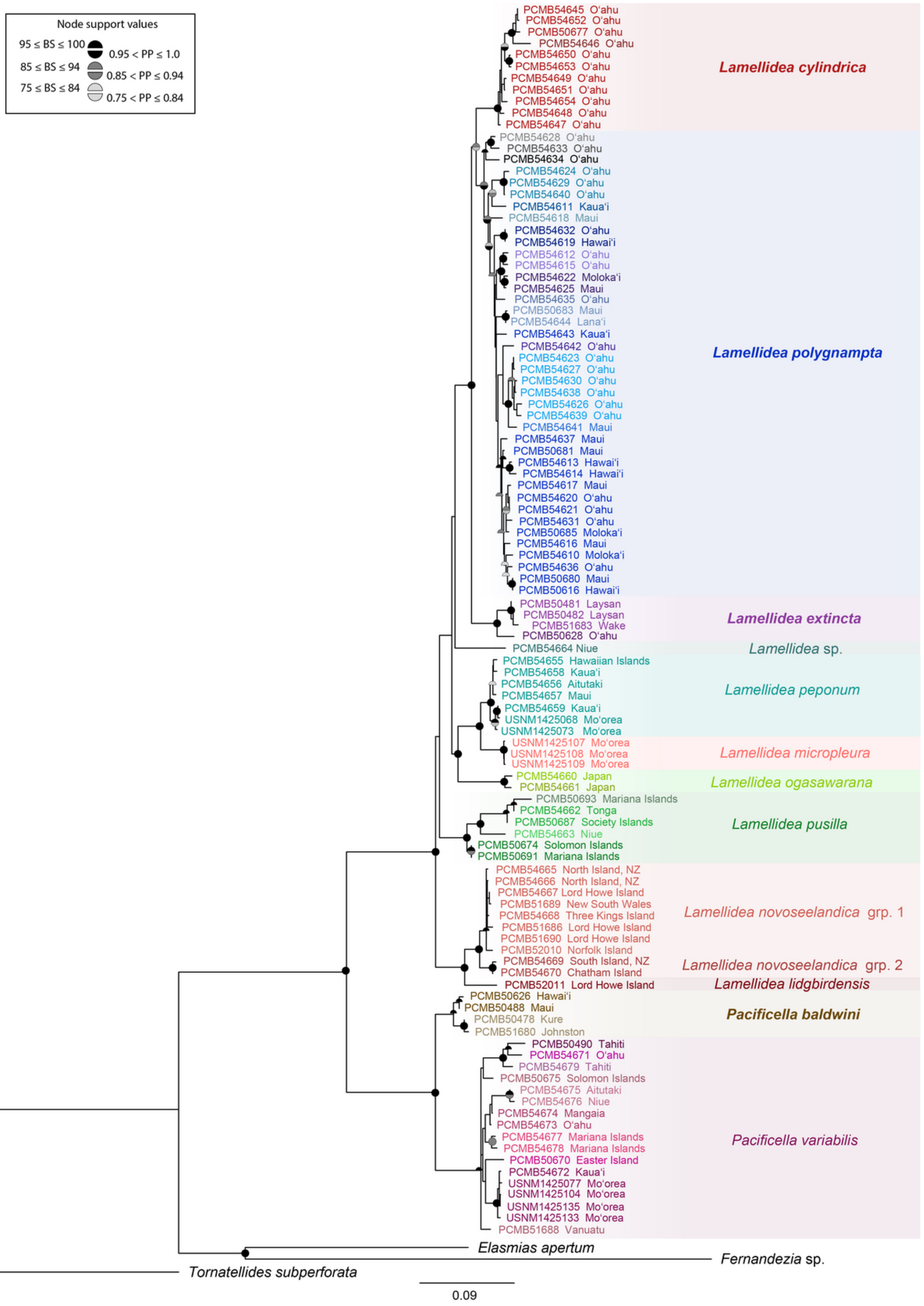


Figure 2. Phylogenetic tree based on partial COI, 16S, 28S, and ITS2 sequences with localities and final species identifications.

Bootstrap support and posterior probabilities are indicated by shaded circles at the nodes. The colors used for specimens in the tree are the same as in Figure 1. The names of Hawaiian pacificelline species are indicated in bold.

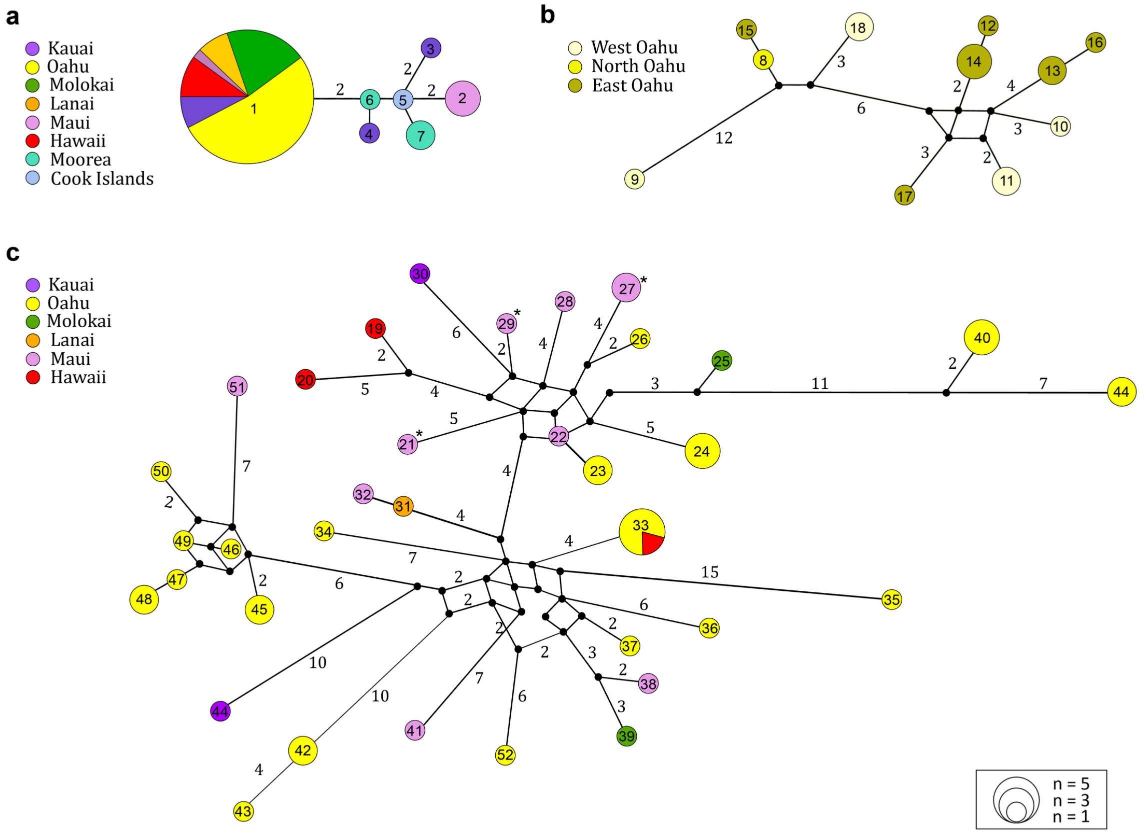


Figure 3. Median-joining networks based on partial COI sequences.

Colored circles represent unique haplotypes, numbers inside the circles identify the haplotype number of the individual(s) sequenced (see Table 2), and the size of the circle is scaled to the number of individuals. Numbers beside the branches indicate the number of mutational steps. (a) *Lamellidea peponum* (N = 50) (b) *Lamellidea cylindrica* (N = 17) (c) *Lamellidea polygnampta* (N = 50). * indicates topotypic haplotypes.

Society Islands (Figs. 1, 2), which are separated by few mutational differences as shown on the haplotype map (Fig. 3a).

Tornatellinops novoseelandica (Küster, 1852) from New Zealand and the surrounding islands, the Three Kings Islands to the north, and Chatham Island to the east is not monophyletic with respect to *T. inconspicua* (Brazier, 1872) from Lord Howe Island, *T. jacksonensis* (Cox, 1864) from eastern Australia, and *T. norfolkensis* (Preston, 1913) from Norfolk Island in multilocus phylogenetic analyses (Fig. 2) or in analyses of COI sequences (Fig. 1a). In the mitochondrial phylogeny, the relationship between *T. novoseelandica* and *T. lidgbirdensis* is an unresolved polytomy (Fig. 1a), but they are recovered as sister taxa in multilocus analyses (Fig. 2). Species delimitation analyses all recover individuals from northern New Zealand (North Island, Three Kings Islands), Lord Howe Island, and New South Wales (*novoseelandica* group 1) as a separate species to individuals from southern New Zealand (South Island and Chatham Island, *novoseelandica* group 2), and to *T. lidgbirdensis* (Fig. 1a).

The *Lamellidea pusilla* clade is strongly supported (BS 99, PP 1) but has high intraspecific divergence in COI (up to 10.3%). The relationship of *L. pusilla* to other Polynesian and South Pacific *Lamellidea* species is unsupported in the mitochondrial (BS 67) and multilocus analyses (BS 58, PP 0.53).

3.2 Geographic and elevational distributions

A significant difference ($p<0.05$) was observed in the mean elevational distribution of *L. polygnampta* (814 meters) and the species *L. extincta*, *L. cylindrica*, *L. peponum,* and *P. variabilis*, which were recorded at lower mean elevations (11, 287, 286, and 42 meters respectively) (Fig. 4C).

3.3 New records and taxonomic changes

Two species are recognized here in the genus *Pacificella* Odhner, 1922: the type species, *Pacificella variabilis* Odhner, 1922, distributed across the islands of the Pacific, and *Pacificella baldwini* (Ancey, 1889), known only from the Hawaiian Islands and nearby atolls in the central Pacific. *Pacificella variabilis* is recorded in the Hawaiian Islands for the first time, with individuals from Oʻahu and a horticultural facility on Kauaʻi and genetically similar specimens from the South Pacific. *Pacificella baldwini rugosa* (Pilsbry & Cooke, 1915) and *P. mcgregori* (Pilsbry & Cooke, 1915) from the Hawaiian Islands are synonymized with *Pacificella baldwini*, as the shell morphology of these subspecies is within the range of variation observed in *P. baldwini*.

One clade within the Pacificellinae includes species of *Lamellidea* Pilsbry, 1910 and *Tornatellinops* Pilsbry & Cooke, 1915, including the type species of both genera. The name *Lamellidea* has taxonomic priority, and the name

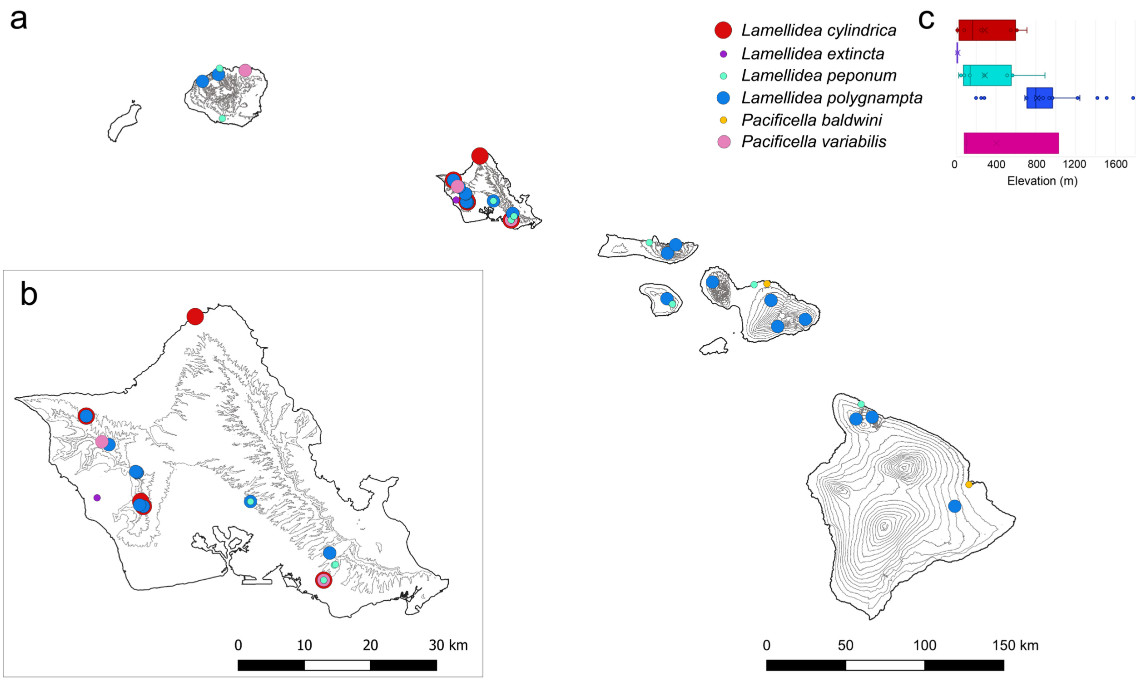


Figure 4. Map of sampling localities of sequenced Pacificellinae by species.

Contour lines indicate 250 meter intervals. (a) Species from the high islands of Hawaiʻi (b) Detailed view of species on Oʻahu (c) Elevation of sequenced *Lamellidea* specimens in Hawaiʻi. The "x" indicates the mean, and the box indicates the 25th to 75th percentile.

Tornatellinops is relegated to synonymy. *Lamellidea oblonga* (Pease, 1865), recognized as a widespread species across islands of the Pacific, is a junior synonym of *Lamellidea peponum* (Gould, 1847) from the Hawaiian Islands. The name *Lamellidea gracilis* (Pease, 1871) is also a synonym of *L. peponum*, based on an examination of type material. *Lamellidea gracilis* sensu Pilsbry and Cooke (not of Pease, 1871) is here attributed to *Lamellidea extincta* (Ancey, 1890), formerly considered a junior synonym of *L. gracilis*. The distribution of *L. polygnampta* (Pilsbry & Cooke, 1915) is expanded here to include all of the high islands of Hawaiʻi (Hawaiʻi, Lanaʻi, Maui, Molokaʻi, Oʻahu), and the names *Lamellidea polygnampta kamaloensis* (Pilsbry & Cooke, 1915), *L. lanceolata* (Pilsbry & Cooke, 1915), and *L. tantalus* (Pilsbry & Cooke, 1915) are regarded as junior synonyms.

More than a half-dozen species and subspecies of pacificellines have been recognized from the South Pacific, including *Lamellidea novoseelandica* (Küster, 1852 in Küster, 1841–1855) from New Zealand, *L. jacksonensis* (Cox, 1864) from New South Wales, *L. inconspicua* (Brazier, 1872) from Lord Howe Island, and *L. norfolkensis* (Preston, 1913) from Norfolk Island. Phylogenetic analyses indicate that specimens of these four taxa, all previously attributed to *Tornatellinops*, cluster together in a clade, and they, along with *L. duplicilamellata* (Preston, 1913), *L. norfolkensis moohuensis* (Preston, 1913), *L. norfolkensis nepeanensis* (Preston, 1913), and *L. capricorni* (Iredale, 1944), are recognized herein as synonyms of *L. novoseelandica*. The species delimitation analyses conducted in this study suggest that the two allopatric clades within *L. novoseelandica* may warrant recognition as distinct species. One clade includes individuals from northern New Zealand (northern North Island and the Three Kings Islands) and eastern Australia (New South Wales, Lord Howe Island, and Norfolk Island) while the other clade comprises specimens from southern New Zealand (South Island and the Chatham Islands).

3.4 Systematics of Hawaiian species

- Class Gastropoda Cuvier, 1795
  - Subclass Heterobranchia Burmeister, 1837
    - Order Stylommatophora A. Schmidt, 1855
      - Superfamily Pupilloidea W. Turton, 1831
        - Family Achatinellidae Gulick, 1873
          - Subfamily Pacificellinae Steenberg, 1925

Pacificellinae Steenberg, 1925, p. 195, 202 [as Pacificellidae]. Type genus *Pacificella* Odhner, 1922.

- Lamellideinae Cooke & Kondo, 1961, p. 162. Type genus *Lamellidea* Pilsbry, 1910. **New synonym.**
- Tornatellinoptini Cooke & Kondo, 1961, p. 162. Type genus *Tornatellinops* Pilsbry & Cooke, 1915.

Remarks: Three tribes have been recognized within the Pacificellinae: Pacificellini, Lamellideini, and Tornatellinoptini (Bank, 2017). The Tornatellinoptini was relegated to synonymy with Pacificellini by Bouchet et al. (2017). Here we also synonymize the tribe Lamellideini with Pacificellinae based on morphological similarity of genera within these two taxa.

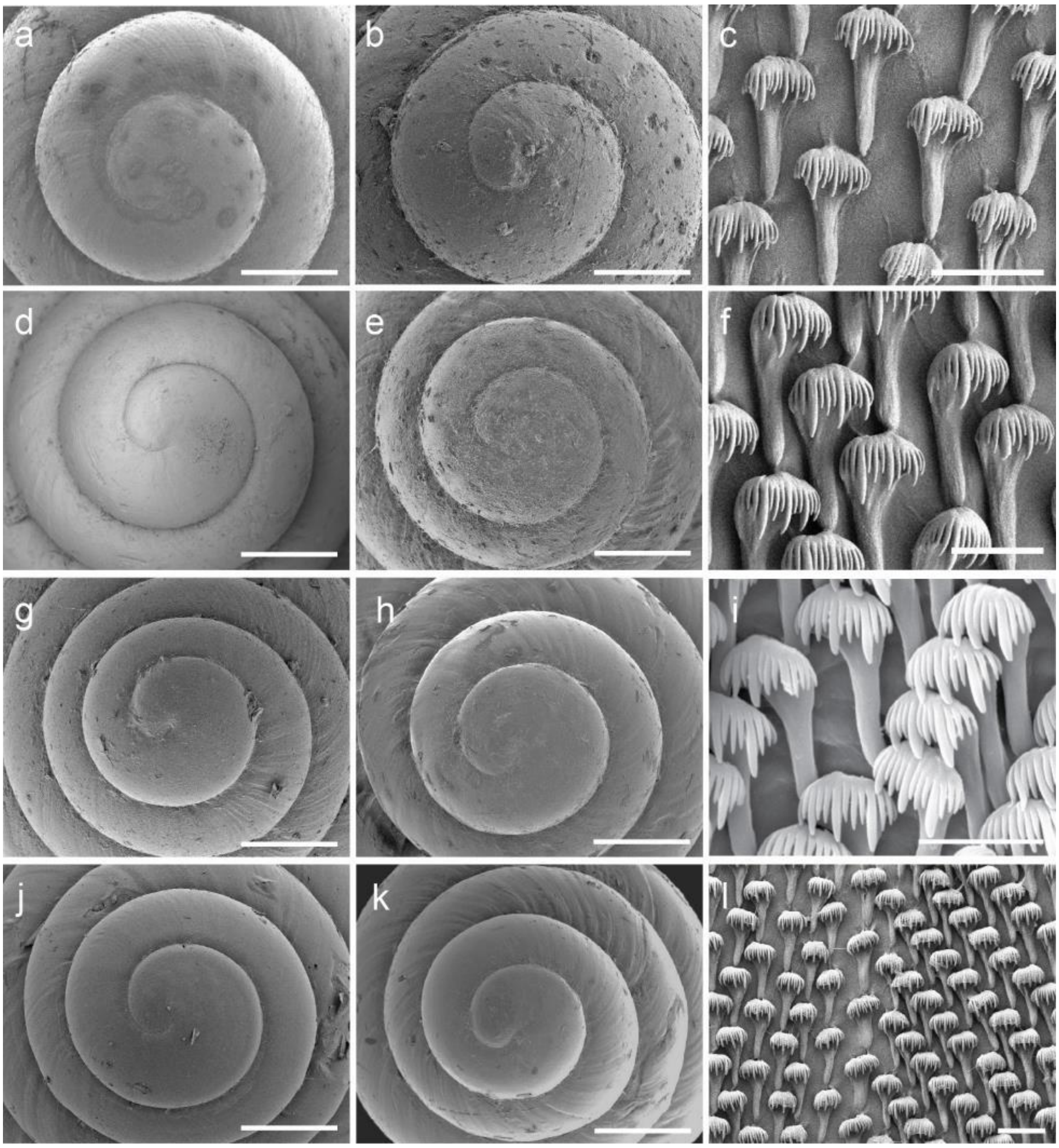


Figure 5. Embryonic whorls and radular morphology of *Lamellidea* and *Pacificella* spp.

(a) Embryonic whorls of *P. variabilis* BPBM 288707 Oʻahu (b) Embryonic whorls of *P. baldwini* BPBM 18610 Maui (c) Marginal teeth of *P. variabilis* BPBM 286835 Kauaʻi (d) Embryonic whorls of *L. peponum* BPBM 270725 Oʻahu (e) Embryonic whorls of *L. cylindrica* BPBM 288706 Oʻahu (f) Marginal teeth of *L. peponum* BPBM 286943 Maui (g) Embryonic whorls of *Lamellidea extincta* BPBM 188760 Oʻahu (h) Embryonic whorls of *L. polygnampta* BPBM 288697 Oʻahu (i) Marginal teeth of *L. cylindrica* BPBM 270663 (PCMB54645) Oʻahu (j) Embryonic whorls of *L. polygnampta* BPBM 288695 Molokaʻi (k) Embryonic whorls of *L. polygnampta* BPBM 288698 Oʻahu (l) Rachidian tooth and marginal teeth of *L. polygnampta* BPBM 288701 Oʻahu. Scale bar of embryonic whorls = 200 µm, scale bar radulae = 5 µm.

Genus Pacificella *Odhner, 1922*

Pacificella Odhner, 1922, p. 249. Type species *Pacificella variabilis* Odhner, 1922, by monotypy.

Diagnosis: Whorls 5 to 6, shell taller than wide, height 2–4 mm, dextral. Protoconch smooth (Fig. 5a), teleoconch smooth with fine growth lines. Parietal lamella present, moderate or inconspicuous.

Radula: Rastriform marginal teeth in v-shaped rows with an irregular central tooth (rachidian). Each marginal tooth is rake-like, with a long narrow basal plate that gradually widens to the broad recurved head bearing approximately 16 narrow cusps between 1/3 and 1/4 the length of the tooth (Fig. 5c). The number of teeth ranges from approximately 100 to 140 per row in specimens of *P. variabilis* from Makiki, Oʻahu (N = 4, Table S3).

Remarks: The genus was established by Odhner (1922) for *Pacificella variabilis* Odhner, 1922, based on material from Easter Island (Rapa Nui). Pilsbry and Cooke (1933, p. 60) and Cooke (1934, p. 9) treated *Pacificella* as a synonym of section *Tornatellinops* Pilsbry & Cooke, 1915 in the genus *Lamellidea* Pilsbry, 1910. Cooke and Kondo (1961, p. 162) treated *Tornatellinops* as a separate genus, with *Pacificella* as a synonym. However, Climo (1973, p. 578) noted that *Tornatellinops novoseelandica,* the type species of this genus, was not a congener of ʻ*T.*ʼ *variabilis*, with Cooke & Kondo (1961) having made an error "in the systematic placement of *Tornatellinops* due to their anatomical information on the genus being based on other than the type species." Schileyko (1998, p. 23) reproduced illustrations of the anatomy of Pacificellinae species by Cooke & Kondo (1961) but incorrectly stated that the anatomy illustrated in

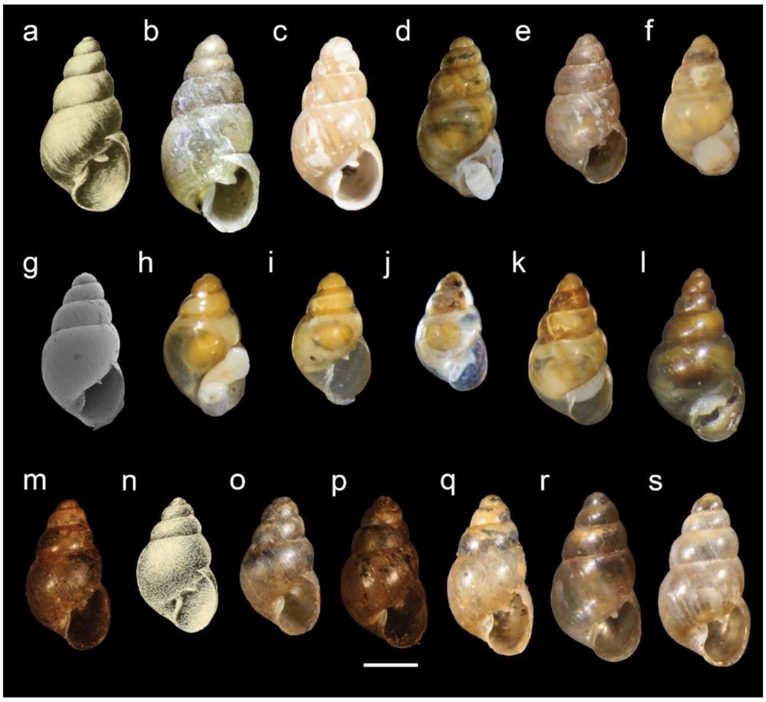


Figure 6. Shells and original illustrations of *Pacificella* spp.

(a) *Pacificella variabilis* Odhner original figure (b) *P. variabilis* Odhner syntype SMNH 1668, photographed by Anna Persson (© 2020 Naturhistoriska riksmuseet). Made available by the Swedish Museum of Natural History under Creative Commons Attribution 4.0 International Public License, CC-BY 4.0 (c) *P. variabilis* BPBM 207570 Easter Island (d) *P. variabilis* BPBM 286835 Kauaʻi (e) *P. variabilis* BPBM 288714 Solomon Islands (f) *P. variabilis* AM C.4482 Vanuatu (g) *P. variabilis* BPBM 288707 Makiki, Oʻahu (h) *P. variabilis* BPBM 288654 Mangaia, Cook Islands (i) *P. variabilis* BPBM 288669 Aitutaki, Cook Islands (j) *P. variabilis* BPBM 288674 Mariana Islands (k) *P. variabilis* BPBM 288708 Moʻorea, Society Islands (l) *P. variabilis* BPBM 288679 Tahiti, Society Islands (m) *P. mcgregori* Pilsbry & Cooke lectotype ANSP 85387 (n) *Tornatellina baldwini* Ancey (1903, pl. 12, fig. 1) (o) *P. baldwini* BPBM 18610 Maui (PCMB50488) (p) *Tornatellina baldwini subrugosa* lectotype ANSP 98050 (q) *P. baldwini* BPBM 25081 Hilo, Hawaiʻi (PCMB50626) (r) *P. baldwini* BPBM 57522 Johnston Atoll (PCMB50673) (s) *P. baldwini* BPBM 288713 Kure Atoll (PCMB50477). Scale bar = 1 mm.

his figure 19 was of *Tornatellinops novoseelandica*, whereas it was actually an illustration of *Pacificella variabilis* (from Cooke & Kondo, 1961, fig. 76). Climo did not indicate how the nomenclature of *T. variabilis* and related species should be modified, stating that "[t]he provision of a name here must await some other worker more familiar than the writer with the intricacies of Cooke and Kondo's systematic hierarchy" (Climo, 1973, p. 578). This taxonomic question was resolved by Cowie et al. (1995), who indicated that *Pacificella* was the earliest available genus-group name for *variabilis* and its congeners: the Hawaiian taxa *baldwini baldwini* (Ancey, 1889), *baldwini subrugosa* (Pilsbry & Cooke, 1915), and *mcgregori* (Pilsbry & Cooke, 1915). Our phylogenetic analyses indicate that *Lamellidea* and *Pacificella* are reciprocally monophyletic, while the genus-group name *Tornatellinops* refers to the same clade as *Lamellidea. Tornatellinops* is therefore a synonym of *Lamellidea*. The *Pacificella* individuals sequenced in this study comprise two species, *P. baldwini* and *P. variabilis*.

Pacificella variabilis ***Odhner, 1922 (Figs. 5a, 5c, 6a–6l)***

Pacificella variabilis Odhner, 1922, pp. 249–252, pl. 8, figs. 13–17.

Syntypes: SMNH 1668 (5 spm) (Fig. 6b); SMNH 6410 (10 spm); ANSP 130441 (4 spm); BPBM 189707 (1 spm). 'Easter Island' (Odhner, 1922, p. 250).

Description: Shell oblong, ovate; parietal lamella small to moderate.

Distribution: Widely distributed in the Pacific, from Marianas and Caroline Islands east to Easter Island (Cooke & Kondo, 1961; Cowie, 2000), and recorded here for the first time from Hawaiʻi.

Ecology: Primarily a low elevation species, arboreal and ground-dwelling. On Easter Island, the species lives in the endemic grass *Paspalum forsterianum,* and it has also been found on the bark of a lemon tree (Araya et al., 2018). In the Cook Islands, this species is present in a wide variety of coastal and near-coastal habitats, including herbaceous strand vegetation, shrubland and forest remnants, and highly modified, open, anthropogenic habitats, living on ferns and the trunks, stems, and leaves of shrubs and trees, and on the ground among fallen leaves and dead wood (Brook, 2010). Most specimens used in DNA analyses were collected between 0 and 120 meters elevation (Mariana Islands 120 m, Solomon Islands 1–10 m, Vanuatu 34 m, Niue 20 m, Cook Islands 37–38 m, Moʻorea 2–8 m), although a specimen from Tahiti was collected in a ginger patch with *Pisonia* sp. and various ferns at 230 meters elevation. Specimens from Hawaiʻi were collected from leaf litter in a residential park on Oʻahu at low elevation (80 meters), from a plant nursery on Kauaʻi (ca. 100 meters), and in leaf litter in the Mt. Kaʻala Natural Area Reserve under *Metrosideros polymorpha* at 1,028 meters.

Remarks: The original description of *Pacificella variabilis* was based on material collected on Easter Island (Fig. 6a). Cooke & Kondo (1961, p. 173, fig. 77) illustrated the distribution of this species as extending from Tuvalu to Easter Island, but in the text (1961, p. 173), they expanded the western limit of the species to Truk in the Caroline Islands. Noting the close similarity of shells across several island groups of the central Pacific, Cooke & Kondo (1961, p. 173) suggested that the wide distribution of this species was at least in part anthropogenic. Pilsbry & Cooke (1933, p. 60) considered that *P. variabilis* was introduced to Easter Island, "doubtless by the Polynesians, as we have found shells completely identical with those of Easter Island in several Polynesian localities," but Cooke & Kondo (1961) concluded that, while humans probably contributed to the dispersal of the species to low islands and atolls, "whether the species was dispersed by man or nature cannot be determined." Analyses of fossil shells of Henderson Island, Pitcairn Group suggest that the species was present in the islands before the arrival of humans in the islands (Preece, 1998). The species is present at archaeological sites in the Marshall Islands and Easter Island, and in paleosols on Rarotonga, Cook Islands, but the timing of its arrival in these islands has not been resolved (Brook, 2010; Christensen & Weisler, 2013; Kirch et al., 2009).

For the present study, we obtained sequence data from museum specimens of *P. variabilis* from the type locality, Easter Island (Fig. 6c), and specimens identified as *P. variabilis* from other islands in the South Pacific. Although not recorded previously from the Hawaiian Islands (Cowie, 2001), several specimens collected from a plant nursery on Kauaʻi in 2017 (BPBM 286835, PCMB54672) were identified as *P. variabilis* based on clustering of DNA sequences with the sequenced topotypes (4.9% divergent in COI) in the mPTP analysis (Fig. 1). The Kauaʻi specimens are most closely related to specimens from French Polynesia (0.6–1.2% in COI), also identified as *P. variabilis*. It is unknown if *P. variabilis* is established on Kauaʻi. Specimens collected below the Koʻolau Mountains of Oʻahu from a park in 2019 (Fig. 6g) are slightly more divergent from the sequenced topotypes (5.8% divergent in COI). These Oʻahu specimens are very closely related (0.6% in COI) to a specimen from Mangaia, Cook Islands (Fig. 6h). Only one *Pacificella* specimen was found in the last 15 years of surveys of native Hawaiian forests, from near the summit of Mt. Kaʻala, Oʻahu (BPBM 288675, PCMB54671). Although this is a high elevation habitat, we note that it is more accessible than many high elevation sites in the Hawaiian Islands. A controlled government road allows access to the mountain peak by vehicles and is traversed by a popular hiking trail. It is unclear if *P. variabilis* is widely distributed throughout the Waiʻanae Mountains, but other introduced snail species have been documented from Mt. Kaʻala (e.g., Curry & Yeung, 2013). *Pacificella variabilis* has not been recorded in archaeological or pre-human fossil land snail assemblages in the Hawaiian Islands and is evidently a recent introduction, although the precise timing is difficult to determine due to the morphological similarity to *P. baldwini*.

As the name implies, the species is highly variable in shell morphology, with many islands characterized by "distinct forms or subspecies" (Cooke & Kondo, 1961, p. 173). The specimens sequenced for this study vary in shell height and number of whorls, with the smallest from the Mariana Islands and the largest from Easter Island. Despite these size differences, the smallest specimens from the Mariana Islands and the Cook Islands (Figs 6i–6j) are reproductively mature, as evidenced by the presence of large embryos visible through the thin shells. The DNA sequence from the specimen collected at high elevation (BPBM 288675) is most closely related to *P. variabilis* from Tahiti. The specimen from Tahiti tapers slightly more than other specimens in this study, with shouldered whorls (Fig. 6k). One individual from Tahiti, BPBM 288679, is more tapered in shape and similar in shape to *L. pusilla* (Fig. 6l) but clustered with *P. variabilis* in phylogenetic analyses (Fig. 1a, Fig. 2).

Pacificella baldwini *(Ancey, 1889) (Figs. 5b, 6n–6s)*

Tornatellina baldwini Ancey, 1889, pp. 238–239.

- *Tornatellina baldwini subrugosa* Pilsbry & Cooke, 1915, pp. 143–144, pl. 35, figs. 7, 10. **New synonym.**
- *Tornatellina mcgregori* Pilsbry & Cooke, 1915, p. 144, pl. 35, figs. 14–15. **New synonym.**

Holotype: by monotypy. Whereabouts not known (see below). H = 2.5 mm. 'Tantalus, dans l'ile d'O'ahu' (Ancey, 1889, p. 238).

OTHER TYPE MATERIAL

Lectotype (*T. baldwini subrugosa*): (Baker, 1963, p. 196) ANSP 98050a (Fig. 6p). H = 2.8 mm. *Paralectotypes*: ANSP 419077 (4 spm). Maui.

Lectotype (*T. mcgregori*): (Baker, 1963, p. 195) ANSP 85387a (Fig. 6m). H = 2.8 mm. *Paralectotypes* ANSP 419078 (79 spm). 'Hawaii, Hilo'.

Description: Shell oblong, ovate (up to 3.4 mm); parietal lamella small to moderate.

Distribution: Hawaiian Islands (Oʻahu, Kauaʻi, Maui, Hawaiʻi), Kure Atoll, and Johnston Atoll.

Ecology: Notes on the collection localities of *P. baldwini* in the Bishop Museum collections indicate that some specimens were found on dead hala leaves, guava, ferns, shrubs, or bunch grass. Similarly, *P. mcgregori* was described from specimens collected under guava leaves. Precise habitat information is not available for the specimens sequenced from the BPBM collection. Pilsbry & Cooke (1915 [in 1914–1916], p. 142) indicated that the species was present in the Pleistocene of Oʻahu at Kaelepulu, Kailua, Laie, and 1 ½ miles west of Kahuku. These are all coastal, low elevation sites, and many of the localities of shells of *P. baldwini* in the Bishop Museum collections are also low to mid-elevation, including Kahuku, Kalihi, Nuʻuanu, Manoa, and Waimanalo (Oʻahu), Kalihikai, and Mahaulepu (Kauaʻi), and Waihee (Maui). No living specimens were found during extensive surveys of Oʻahu and the neighboring islands.

Remarks: Tornatellina baldwini was described from a single specimen (H = 2.5 mm) that was stated to have been collected by Baldwin from Tantalus, Oʻahu (Ancey, 1889, p. 238). Ancey later indicated that the specimen described was not fully developed and provided an illustration of a mature individual (1903: pl. 12, figs. 1, 2 shown in Fig. 6n). The species was also recorded from three other Hawaiian Islands at that time: Maui (Kaupakalua and Keanae), Hawaiʻi, and Kauaʻi. Pilsbry & Cooke (1915 [in 1914–1916], p. 143) referred to a specimen in the Bishop Museum from Manoa, Oʻahu (BPBM 18422) from Ancey's collection as his type, and other specimens in the BPBM collection (BPBM 18423) from Manoa were labeled as 'cotypes'. However, the specimen in BPBM 18422 (H = 2.7 mm) is not the immature holotype from Tantalus but rather appears to be Ancey's illustrated specimen. We have not been able to locate the holotype in the Bishop Museum collection. Johnson (1996) and Wood & Gallichan (2008) indicated that some of Ancey's type material was traded to the Harvard Museum of Comparative Zoology and The Academy of Natural Sciences, but the holotype has not been located in these collections. It also has not been found at the National Museum of Wales or the Royal Belgian Institute of Natural Sciences, which also houses material from Ancey's collection.

Pilsbry and Cooke (1915 [in 1914–1916], p. 142) added new records of *P. baldwini* from Nuʻuanu and the Waiʻanae Mountains of Oʻahu in the Manual of Conchology. Dried material of *Pacificella baldwini* was not available from Tantalus or nearby localities for DNA isolation, but DNA was sequenced from one of Ancey's dried specimens of *P. baldwini*, BPBM 18610 from Kaupakalua, Maui (PCMB50488, H = 3.1 mm) and is similar in shape to the specimen from Oʻahu illustrated by Ancey (1903: pl. 12, figs. 1, 2). The sequence from this individual is distinct from *P. variabilis* in all species delimitation analyses (Fig. 1a). Pilsbry and Cooke also described a new variant of *P. baldwini* as *T. baldwini subrugosa* (Fig. 6p), but the locality was given only as Maui in the ledger at ANSP and the description. *Tornatellina baldwini subrugosa* was described as differing from *T. baldwini* in the low folds or wrinkles in the direction of growth striae, but no marked morphological differences are noted from *P. baldwini*; we, therefore, synonymize the name *subrugosa* with *baldwini*.

Pilsbry and Cooke recognized a second *Pacificella* species in the Hawaiian Islands from Hilo, Hawaiʻi, named *T. mcgregori* (ANSP 85387, Fig. 6m), and indicated that the species differed from *T. baldwini* by the less sinuous columella and smaller parietal lamella. No *Pacificella* specimens were found in recent land snail surveys on the island of Hawaiʻi, but a *Pacificella* specimen from the BPBM collection from Hilo, Hawaiʻi (H = 2.7 mm) collected in approximately 1913 was sequenced and found to be closely related to *P. baldwini* from Maui (0.7% divergent in COI). Although the specimen from Hilo has a slightly more sinuous parietal lamella, the overall similarity in shell morphology suggests that *P. mcgregori* represents intraspecific variation within *P. baldwini*, and we therefore synonymize *mcgregori* with *baldwini* here.

Specimens from Johnston Atoll (Fig. 6r, same COI sequence as BPBM 57540) and Kure Atoll (Fig. 6s) are closely related to those from the main Hawaiian Islands (2.0–3.3% divergent in COI sequences). Although the specimens from Kure and Johnston are slightly larger (3.3–3.4 mm in height versus 2.7–3.1 mm) than those from Maui and Hawaiʻi, ASAP #9 and mPTP species delimitation analyses suggest that they are a single species. Based on these species delimitation analyses and the intraspecific variability in shell morphology of other pacificelline species, we consider the specimens from the Northwestern Hawaiian Islands to belong to *P. baldwini*.

Genus Lamellidea *Pilsbry, 1910*

Tornatellina (*Lamellidea*) Pilsbry, 1910, p. 123. Type species *Pupa peponum* Gould, 1847, by original designation.

- *Lamellina* Pease, 1861, p. 439. Invalid: junior homonym. Type species *Lamellina serrata* Pease, 1861.
- *Lamellaria* Liardet, 1876, p. 101. Invalid: junior homonym. Type species *Pupa peponum* A. Gould, 1847.
- *Tornatellinops* Pilsbry & Cooke, 1915, p. 162. **New synonym.** Type species *Tornatellina novoseelandica* Küster, 1852, by original designation.
- *Lamellidea* (*Atea*) Pilsbry & Cooke, 1933, p. 62. Invalid: junior homonym. Type species *Lamellidea adamsoni* Pilsbry & Cooke, 1933.
- *Tornelasmias* Iredale, 1944, p. 308. **New synonym.** Type species *Tornelasmias capricorni* Iredale, 1944, by original designation.
- *Lamellidea* (*Elamellidea*) Cooke & Kondo, 1961. **New synonym.** Type species *Lamellidea tantalus* (Pilsbry & Cooke, 1915).
- *Lamellidea* (*Auhea*) Kondo, 1962, p. 125. Type species *Lamellidea adamsoni* Pilsbry & Cooke, 1933.

Diagnosis: Whorls 5 to 9, shell taller than wide, height 2–7 mm, dextral. Protoconch smooth, teleoconch smooth with fine growth lines. Parietal lamella present.

Radula: Rastriform marginal teeth in v-shaped rows with an irregular central tooth. Each marginal tooth is rake-like with a long narrow basal plate that gradually widens to the broad recurved head bearing approximately 16 narrow cusps between 1/3 and 1/4 the length of the tooth (Fig. 5f). The number of teeth ranges from approximately 110 to 150 per row (N = 3, Table S3).

Remarks: The Hawaiian Pacificellinae were referred to two genera by Pilsbry & Cooke (1914–1916) and Cooke & Kondo (1961): *Lamellidea* Pilsbry, 1910, type species *Pupa peponum* by original designation [Hawaii], and *Tornatellinops* Pilsbry & Cooke, 1915, type species *Tornatellina novoseelandica* by original designation. *Lamellidea* was previously one of four sections that Pilsbry (1910, p. 123) had recognized in the genus *Tornatellina* Pfeiffer, 1842: *Tornatellina sensu stricto*; *Elasmatina* Petit de la Saussaye, 1843; *Lamellina* Pease, 1861; and *Lamellidea* Pilsbry, 1910. *Lamellidea* was treated as a synonym of *Lamellina* by Pilsbry & Cooke (1915 [in 1914–1916], p. 150), but, after realizing the latter to be a junior homonym of *Lamellina* Bory de Saint-Vincent, 1824 [Protozoa], they reinstated *Lamellidea* (Pilsbry & Cooke, 1916 [in 1914–1916]: 273). For *Lamellidea*, Cooke & Kondo (1961) established the subfamily Lamellideinae Cooke & Kondo, 1961, a junior synonym of Pacificellinae Steenberg, 1925, as noted by Cowie et al. (1995, p. 78). Cooke & Kondo's (1961, p. 181) classification of *Lamellidea* was based on shell morphology and internal anatomy of representative species. Their classification included seven species endemic to Hawai'i (*L. cylindrica*, *L. gayi*, *L. gracilis*, *L. lanceolata*, *L. peponum*, *L. polygnampta*, and *L. tantalus*), the Polynesian species *L. oblonga* (Pease, 1865), *L. micropleura* Cooke & Kondo, 1961, and the Pacific-wide *L. pusilla* group comprising seven species: *L. biplicata* (Pilsbry, 1902)*, L. microstoma* (Möllendorff & Quadras, 1894)*, L. ogasawarana* (Pilsbry & Cooke, 1915)*, L. pusilla* (Gould, 1847), *L. solomonensis* Dell, 1955, and *L. subcylindrica* (Möllendorff & Quadras, 1894). According to Cooke & Kondo (1961, pp. 24–26), *Lamellidea* has a wide distribution in the Pacific, from Ogasawara and the Caroline Islands east to Hawai'i and the Pitcairn Islands, but is absent from the South Pacific west of Fiji; although, their inclusion of *Lamellidea solomonensis* from the Solomon Islands contradicts this.

Cooke & Kondo (1961) established *Elamellidea* as a subgenus of *Lamellidea* with *L. tantalus* as the type. This nominal species is treated as a synonym of *L. polygnampta* here. As part of the *Lamellidea* clade including the type species *Lamellidea peponum*, *Elamellidea* is synonymized here with *Lamellidea*.

Tornatellinops was established as a section of *Tornatellina*, with the New Zealand species *Tornatellina novoseelandica* as the type. *Tornatellinops* was treated as a separate genus by Iredale (1937) and Cooke & Kondo (1961) and extensively revised by the latter authors to include a total of 22 species from Australia, New Zealand, and islands across the Pacific. The group was considered a subgenus of *Lamellidea* by Thiele (1931 [in 1929–1931], p. 497), Zilch (1959, p. 132), and Climo (1973, p. 578). However, the treatment of *Tornatellinops* as a subgenus of *Lamellidea* has not been widely adopted, and most publications on Australian Pacificellinae have continued to use *Tornatellinops* at the rank of genus (e.g., Brook, 1999; Powell, 1979; Smith, 1992; Spencer et al., 2009; Spencer & Willan, 1996; Stanisic et al., 2010). The molecular phylogeny reconstructed here shows that *T. novoseelandica* belongs to the same clade as *Lamellidea peponum* and supports the synonymy of *Tornatellinops* with *Lamellidea*.

Representatives of the types of two available genus-group names were not included in our analyses. *Tornelasmias* was established for three species of achatinellids from Lord Howe Island, with *T. capricorni* as the type species. *Tornelasmias* was treated as a synonym of *Tornatellinops* by Cooke & Kondo, 1961, p. 162), and thus we provisionally interpret it as a synonym of *Lamellidea*. We follow Bank (2017) in including *Auhea* in the synonymy of *Lamellidea*.

Lamellidea peponum *(Gould, 1847) (Figs. 5d, 5f, 7a–7j, 8a)*

Pupa peponum Gould, 1847, p. 197. Gould, 1856, pl. 7, fig. 104.

- *Tornatellina oblonga* Pease, 1865, p. 673. **New synonym.**
- *Tornatellina bacillaris* Mousson, 1871, p. 16. **New synonym.**
- *Tornatellina dentata* Pease, 1871, p. 460. **New synonym.**
- *Tornatellina gracilis* Pease, 1871, p. 460. **New synonym.**

Lectotype: USNM 5506 (Fig. 7a). H = 3.25 mm. *Paralectotype*: USNM 5506a (1 spm). 'Sandwich Islands' (Gould, 1847, p. 197); 'Sandwich Islands. Hilo, O'ahu' (Gould, 1852, p. 94).

OTHER TYPE MATERIAL

Lectotype (*T. oblonga*): MCZ 154941 (Fig. 7b). H = 3.2 mm. *Paralectotypes*: MCZ 297947 (>25 spm). 'Islands of the Central Pacific' (Pease, 1865, p. 668); 'Tahiti' (Pease, 1871, p. 473); 'Huaheine' (Garrett, 1884, p. 81).

Lectotype (*T. dentata*): MCZ 28918. H = 2.5 mm. *Paralectotypes*: MCZ 175730 (>25 spm). 'Insula Hawaii' (Pease, 1871, p. 460).

Lectotype (*T. gracilis)*: MCZ 302554 (Fig. 7c). H = 3.8 mm. *Paralectotypes*: MCZ 28919 (9 spm). 'Insula Kauai' (Pease, 1871, p. 460).

Description: Shell elongate, tapering, up to 7 whorls; parietal lamella moderate to small. Two developing embryos observed by micro-CT (Fig. 8a).

Distribution: Hawaiian Islands (Hawai'i, Kaua'i, Maui, Moloka'i, O'ahu), Cook Islands, and the Society Islands. It has also been reported from elsewhere in French Polynesia (Austral Islands, Gambier Islands, Marquesas Islands, Rapa Iti, Tuamotu Islands), Fiji, Kiribati (Flint), Line Islands, Pitcairn Islands, American Samoa, Tonga, Tuvalu (Ellice Islands), and Wallis and Futuna (Horne Islands) (Cooke & Kondo, 1961; Preece, 1998), but some of these records may pertain to the *Lamellidea* sp. from Niue (see below).

Ecology: Lamellidea peponum only appears in the very recent fossil record of many archipelagos in the Pacific with the appearance of human settlements (as *L. oblonga* in Preece, 1998; Rolett, 1992) and was present in Hawai'i before European contact (Kirch, 1982). It is believed that the species arrived in the Hawaiian Islands with food plants brought by Polynesians, as no specimens have been identified (as *L. oblonga* or *L. peponum*) from Pleistocene or early-mid Holocene fossil beds (Cooke & Kondo, 1961, p. 202; Dixon et al., 1997; C. Christensen, pers. comm.). In the Hawaiian Islands, this species is found in leaf litter, under rocks, or on shrubs in areas with non-native vegetation (such as pine forest) and in areas near human habitation. Gould (1847, p. 197, 1852, p. 94) stated that *L. peponum* was "very abundant on pumpkin vines" while Cooke & Kondo (1961, p. 200) indicated that *L. oblonga* was "very abundant on and under dead leaves of coconut, pandanus, breadfruit,

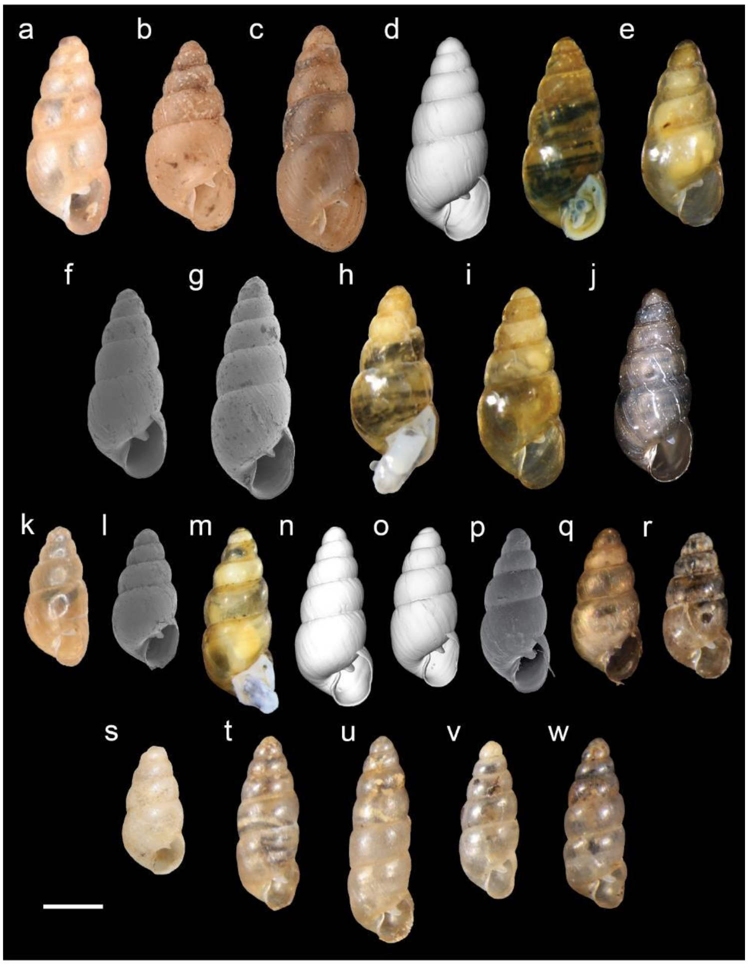


Figure 7. Shells of *Lamellidea* spp.

(a) *Pupa peponum* lectotype USNM 5506 (b) *Tornatellina oblonga* lectotype MCZ154941 (c) *Tornatellina gracilis* lectotype MCZ302554 (d) *L. peponum* BPBM 287046 Kaua‘i (micro-CT scan and photo) (e) *L. peponum* BPBM 288668 Kaua‘i (f) *L. peponum* BPBM 287133 Moloka‘i (COI haplotype same as PCMB54655) (g) *L. peponum* BPBM 286943 Maui (h) *L. peponum* BPBM 286943 Maui (i) *L. peponum* BPBM 288670 Cook Islands (j) *L. peponum* USNM 1425073 Mo‘orea (k) *Tornatellina cylindrica* lectotype NHMUK 1900.12.18.128 (l, m) *L. cylindrica* BPBM 288706 O‘ahu (n) *Lamellidea cylindrica* BPBM 288696 O‘ahu (o) *L. cylindrica* BPBM 288704 O‘ahu (p) *L. cylindrica* BPBM 288662 O‘ahu (q) *L. cylindrica* BPBM 270663 (PCMB54645) O‘ahu (r) *L. cylindrica* BPBM 182809 O‘ahu (s) *Tornatellina extincta* syntype BPBM 18429 (t, u) *L. extincta* BPBM 18876 O‘ahu (v) *L. extincta* BPBM 22747 Laysan (w) *L. extincta* BPBM 189607 Wake Island. Scale bar = 1 mm.

and other plants lying on the ground. It is often taken on stones, but rarely found near the bases of tree trunks and even less often on the leaves of growing shrubs and ferns.” Cooke & Kondo (1961, p. 200) further noted that museum specimens of *L. oblonga* were not collected from native forests. Specimens collected for this study were from non-native and modified habitats, consistent with Cooke & Kondo’s findings. In the early twentieth century, *L. peponum* was abundant (some BPBM lots included more than 100 specimens), but the species was found in low abundance in our surveys.

Lamellidea peponum was recorded from Samoa by Schmeltz (1866, p. 29). Later authors including Cowie (1998, p. 48) recognized the species in Samoa as *L. oblonga*, and *L. peponum* as endemic to Hawai‘i (Cooke & Kondo, 1961, p. 210; Cowie et al., 1995, p. 80). Garrett (1879, p. 21) reported that *Lamellidea peponum* [as *oblonga*] was present from sea level to over 610 meters (2000 feet) elevation in the Austral Islands. Cooke & Kondo (1961, p. 200) noted that few specimens at BPBM had been collected above 305 meters (1000 feet) elevation, and they considered that this species was “more or less confined to the lowlands.” Individuals of *L. peponum* collected alive in Hawai‘i over the last 15 years were found at 18 sites with elevations of between 24 m and 892 m, showing that this species is not restricted to low elevations, although the mean elevation of the localities where it was found was 286 meters (Fig. 4).

Remarks: Pupa peponum was originally described from a mixed lot of specimens containing three achatinellid species (Sykes, 1903, p. 382). Gould indicated that his type material was collected from two localities, and included specimens from O‘ahu collected by Brackenridge and specimens from Hilo collected by Wilkes. Gould’s illustration (1856: pl. 7, fig. 104; reproduced in Yeung et al., 2017, fig. 1F) was identified by Pilsbry and Cooke (1915 [in 1914–1916], p. 157) as corresponding to USNM 5506, which they designated as the lectotype of *peponum*. The USNM label accompanying the lectotype states that the “holotype” of *P. peponum* was collected by Brackenridge, suggesting that O‘ahu may be the type locality, but the USNM ledger entry does not distinguish between the locality of the lectotype and paralectotype; the locality for both specimens

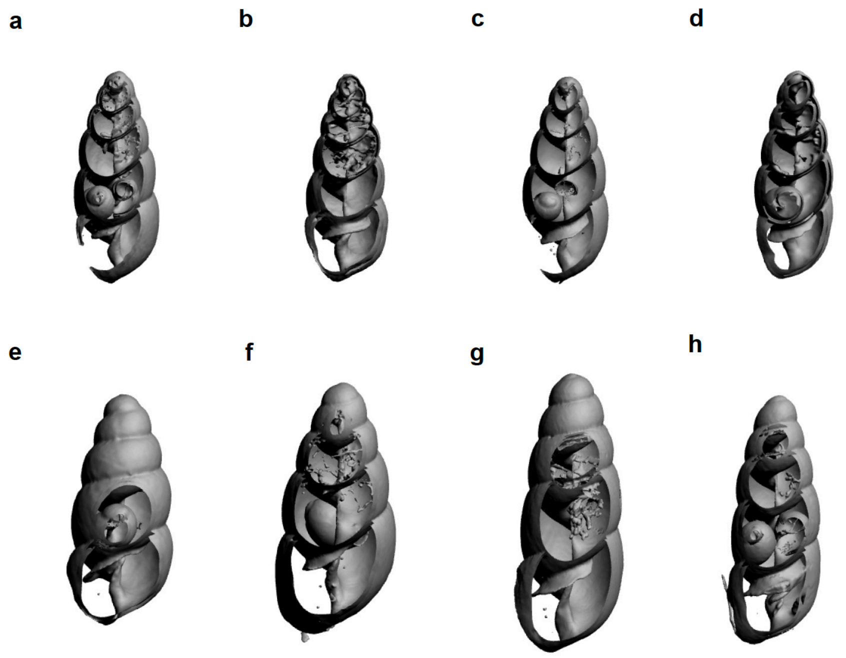


Figure 8. Micro-CT images of Hawaiian Lamellidea species, showing presence or absence of developing embryos

(a) Lamellidea peponum PCMB54658 (BPBM 287046) (b) L. cylindrica PCMB54648 (BPBM 288696) (c) L. polygnampta PCMB54617 (BPBM 288681) (d) L. polygnampta PCMB54623 (BPBM 288700) (e) L. polygnampta PCMB54628 (BPBM 288698) (f) L. polygnampta PCMB54629 (BPBM 288703) (g) L. polygnampta PCMB54625 (BPBM 288694) (h) L. polygnampta PCMB54635 (BPBM 288691). A 3D interactive version of this figure is available in the supplemental material. Micro-CT images of additional specimens are available at http://morphobank.org/permalink/?P565.

is listed as "Sandwich Islands." Gould's lectotype is approximately 3.25 mm in height, which is within the margin of error for Gould's measurement of 3.4 mm (mistakenly reported as 2.5 mm by Yeung et al., 2017). Specimens matching the dimensions and description of Gould's lectotype were sequenced in this study (Figs. 7d & 7e). Pilsbry and Cooke also illustrated a specimen of *L. peponum* from Maui measuring 3.8 mm in height, which closely matches the largest specimen sequenced here, also from Maui (Fig. 7h).

Pease (1865) described *Tornatellina oblonga* without indicating a specific locality in the Central Pacific, but he subsequently (1871, p. 473) wrote that the species was from Tahiti. However, Garrett (1884, p. 81) reported that the types he had collected for Pease were from Huaheine (Society Islands). While the MCZ ledger reports the locality of the lectotype as Tahiti, Pilsbry and Cooke (1914–1916, p. 162) followed Garrett in recognizing the type locality as Huaheine. Pilsbry and Cooke (1914–1916, pp. 157, 161) recorded the species from Hawai‘i as well but noted that "the relationship of *T. peponum* to *T. oblonga* is extremely intimate" and that "adult shells of *T. peponum* and Hawaiian examples of *T. oblonga* do not differ as much as do the young." They further stated that the outer margin of the aperture is more convex in *L. peponum* and somewhat flattened in *L. oblonga*. Examination of material sequenced in this study from the Society Islands, Cook Islands, and the Hawaiian Islands indicates that this character varies within the species (Figs.7d–7j).

The type material of *Tornatellina gracilis* Pease, 1871, which was collected on Kaua‘i, contains two species, as noted by Pilsbry and Cooke (1915 [in 1914–1916], p. 159). These authors interpreted one of the two species as corresponding to *gracilis* and the other as *L. oblonga*. Johnson designated a lectotype of *gracilis* (1994, p. 15, pl. 4, fig. 10) and, unfortunately, selected one of the '*oblonga*' specimens rather than '*gracilis*' *sensu* Pilsbry & Cooke (1915). Accordingly, *T. gracilis* Pease, 1871 is treated here as a synonym of *L. peponum* (Gould, 1847).

Phylogenetic analyses based on COI sequences (Fig. 1a) show little genetic divergence between specimens of *L. peponum* from Hawai‘i and those from Aitutaki, Cook Islands (0.6–0.9%), and between Hawai‘i and Mo‘orea, Society Islands (0.3–1.3%), despite these island groups being separated by over 4,000 km of ocean. However, divergence was observed in nuclear ITS2 sequences (1.6–1.9%) between populations from the Hawaiian Islands and Mo‘orea (Fig. 1b). The genetic diversity of *L. peponum* is quite low in Hawai‘i with most specimens sharing the same COI haplotype (39 specimens shared the same COI haplotype as PCMB54655, Fig. 3a), consistent with recent colonization by a small number of individuals. Overall, the genetic data substantiate previous work suggesting that *L. peponum* (previously recognized as *L. oblonga*) is not native to Hawai‘i.

Lamellidea peponum is similar in appearance to *Lamellidea* sp. from Alofi, Niue but differs substantially genetically (7.9–8.9% divergence) at COI, and the two are not closely related. Further sequencing of *Lamellidea* from Niue and nearby islands is needed to refine the geographic distributions of these two species.

Lamellidea cylindrica *(Sykes, 1900) (Figs. 5e, 5i, 7k–7r, 8b)*

Tornatellina cylindrica Sykes, 1900, p. 381, pl. 11 fig. 28.

Lectotype: NHMUK 1900.12.18.128 designated here. H = ca. 2.4 mm (Fig. 7k). *Paralectotypes*: NHMUK 1900.12.18.129-130 (2 spm), H = 2.7 mm and 2.6 mm. Waianae Mts., Oʻahu. *Paralectotypes*: NHMUK 1900.12.18.1590 (1 spm). Makaweli, Kauaʻi.

Description: Shell small (2.2–3.0 mm), tapered; parietal lamella small to moderate. Two developing embryos observed by micro-CT (Fig. 8b).

Distribution: Oʻahu and possibly Kauaʻi

Ecology: Pilsbry and Cooke (1914–1916, p. 153) reported that *L. cylindrica* was found underneath the bark of *Metrosideros polymorpha* (ʻōhiʻa) and from leaf siftings. The specimens collected for this study were primarily ground-dwelling and living in leaf litter. The species is represented in the Bishop Museum collections by only a few lots, many of which include only 1–2 specimens, suggesting it was already at low abundance in the early to mid-1900s when most specimens were collected. The presence of many introduced species that prey on snails in their habitats together with the low numbers found in recent surveys indicates that the species may be threatened. Individuals collected during surveys in the Hawaiian Islands over the last fifteen years were found at relatively low to moderate elevations, from 10 to 710 meters. Two historical specimens (e.g., Fig. 7r, previously identified in the BPBM collection as *L. gracilis*), sequenced from the Waiʻanae Mountains were collected at approximately 2000 feet elevation (ca. 610 meters).

Remarks: The type material of *Tornatellina cylindrica* includes minute shells, ca. 2.2 mm in height and 1 mm wide. Sykes (1900, p. 381) recorded *Lamellidea cylindrica* from Oʻahu as well as one specimen from Makaweli, Kauaʻi (now known as Kaumakani). However, Pilsbry and Cooke (1914–1916, p. 154) indicated that they had not verified the locality in Kauaʻi, and we found no specimens of *L. cylindrica* in our surveys there. In the BPBM collections, specimens identified as *L. cylindrica* are all from Oʻahu. To clarify the identity of *L. cylindrica*, a lectotype of *L. cylindrica* is selected from the syntypes from the Waiʻanae Mountains (Fig. 7k). The lectotype is the closest in size (H = 2.4 mm) to Sykes' measurement of the species (2.2 mm) of the three syntypes from Oʻahu at the Natural History Museum. The whorls of the lectotype are similar in appearance to Sykes' illustration while the whorls of the two paralectotypes are slightly more convex. The lectotype differs from the illustration in possessing a more flattened apex.

Sykes' NHMUK types are between 2.4 and 2.7 mm in height. The specimens sequenced here have shells between 2.4 (Fig. 7l) and 3.1 mm (Figs. 7m, 7n) in height. The original illustration of *cylindrica* by Sykes (1900: pl. 11, fig. 28) and the lectotype both have a fairly small parietal lamella similar in size to specimens in the clade identified here as *L. cylindrica*, except for the historical specimen (BPBM 288662) which has a larger parietal lamella (Fig. 7p). The bPTP and mPTP delimitation analyses both recognize the sequenced individuals as a single species, while ASAP analyses suggest that the specimens identified here as *L. cylindrica* could represent between 2 species (ASAP #9) and 7 species (ASAP #2). There is variation in shell morphology within *L. cylindrica*, including the size of the parietal lamella, but no obvious fixed differences between the groups identified in the species delimitation analyses. Based on the current data we recognize these specimens as a single species.

Sykes's specimen from Kauaʻi is approximately 2.6 mm in height with a small parietal lamella, less tapered and more cylindrical compared to the species recognized here. At low elevation sites, including a survey in Kalāheo close to Kaumakani (Makaweli), the only *Lamellidea* species found was *L. peponum* (BPBM 287046), but Sykes' specimen is narrower than *L. peponum*. The subspecies *L. cylindrica kilohanana* from Molokaʻi was not found in recent surveys; thus, its validity and relationship to other Hawaiian *Lamellidea* species could not be evaluated here.

Lamellidea extincta *(Ancey, 1890) (Figs. 5g, 7s–7w)*

Tornatellina extincta Ancey, 1890.

Tornatellina gracilis Pease – Pilsbry & Cooke, 1915, pp. 159–160, pl. 42, fig. 11, pl. 43, figs. 7–9.

Syntypes: BPBM 18429 (9 spm), (Fig. 7s), BPBM 41238 (1 spm). Maui. MCZ 175725 (12 spm). Kaupahula, East Maui.

Description: Shell elongate, narrow (ca. 1 mm) tapering, up to 7 whorls; parietal lamella large.

Distribution: Hawaiian Islands (Hawaiʻi, Kahoolawe, Kauaʻi, Kure, Lanaʻi, Lisianski, Maui, Molokaʻi, Nihoa, Niʻihau, and Oʻahu) and Wake Island (Cooke & Kondo, 1961, p. 211; Pilsbry & Cooke, 1914–1916, p. 159).

Ecology: Specimens analyzed here from Laysan Island were collected on bark near the roots of bushes. Cooke & Kondo noted that the species is abundant in lowland fossil deposits and inferred that it is primarily a lowland species. The individuals sequenced in this study from Laysan and Wake Islands were collected from less than 12 meters elevation. Specimens from Lualualei, Oʻahu were collected from under coral rock, where the shells had been deposited by the fire ant *Solenopsis geminata* at roughly 15 meters elevation. The lowland habitats where this species was formerly present have been heavily impacted by introduced species and the loss of native habitats, and in field surveys no individuals of this species were found.

Remarks: The type material of *Tornatellina gracilis* Pease, 1871 comprised a mixture of two species. The lectotype designation of Johnson (1994, p. 15, pl. 4, fig. 10) resulted in the synonymy of *gracilis* Pease with *Lamellidea peponum* and left *extincta* Ancey as the oldest available name for the present species.

Ancey (1890, p. 341) described *Tornatellina extincta* from fossil shells obtained on Maui. Pilsbry & Cooke (1915 [in 1914–1916], pp. 159–160) treated this species as a synonym of *Lamellidea gracilis*. The syntypes, which are all subfossils, are small (height 1.1–2.1 mm) and are difficult to identify owing to early stages of diagenesis (Friedman, 1964). Nonetheless, the illustrated syntype (Fig. 7s) is similar in width and has a similar rate of whorl expansion to the specimens analyzed here from Oʻahu (Figs. 7t–7u). The protoconch of *L. extincta* (Fig. 5g) is similar in size to that of *L. cylindrica* (Fig. 5e) and *L. polygnampta* (Fig. 5h), but the teleoconch is characterized by a lesser rate of whorl expansion than the other species. DNA sequences from two specimens misidentified as *L. gracilis* from the Waiʻanae Mountains (BPBM 182809) clustered with *L. cylindrica* in phylogenetic analyses.

No specimens matching *gracilis sensu* Pilsbry & Cooke (1915), or the type material of *Lamellidea extincta* Ancey (1890), were found during recent surveys in Hawaiʻi. DNA was successfully isolated from three lots of museum specimens from Oʻahu, Laysan, and Wake Islands (Figs. 7t–7w). DNA sequences from these specimens are identified as a single species in the mPTP analysis (Fig. 1a), although ASAP and bPTP species delimitation analyses split individuals from Laysan and Wake Island from specimens on the high islands of Hawaiʻi (COI divergence 4.5–6.0%). Specimens from the main Hawaiian Islands and the Northwestern Islands do not differ consistently in morphology (Pilsbry & Cooke 1915 [in 1914–1916], p. 160). Nuclear ITS2 sequences were not available from these historical museum specimens (new primers would be needed to amplify and sequence a shorter fragment from the degraded DNA).

Lamellidea polygnampta *(Pilsbry & Cooke, 1915) (Figs. 5h, 5j–5l, 8c–h, 9)*

Tornatellina polygnampta Pilsbry & Cooke, 1915, p. 155, pl. 41, figs. 1–5, 7, 8.

- *Tornatellina polygnampta kamaloensis* Pilsbry & Cooke, 1915, p. 156, pl. 40, figs. 4, 5. **New synonym.**
- *Tornatellina lanceolata* Pilsbry & Cooke, 1915, p. 158, pl. 43, figs. 4–6. **New synonym.**
- *Tornatellina tantalus* Pilsbry & Cooke, 1915, p. 172, pl. 40, figs. 8–10. **New synonym.**

Lectotype (*T. polygnampta*): (Baker, 1963, p. 196) ANSP 98049 (Fig. 9a). H = 3.3 mm. Maui. *Paralectotypes*: ANSP 98051 (6 spm), ANSP 419075 (1 spm). Maui. ‘Makawao and Kaupakalua’ [Maui] in original description (Pilsbry & Cooke, 1915 [in 1914–1916], p. 155).

Lectotype (*T. polygnampta kamaloensis*): (Baker, 1963, p. 195) ANSP 109951 (Fig. 9b). H = 2.9 mm. *Paralectotypes*: ANSP 419076 (8 spm). ‘Western ravines of Kamalo near the old irrigation ditch’.

Lectotype (*L. lanceolata*): BPBM 13442 designated here (Fig. 9d). *Paralectotype:* BPBM 41234 (1 spm). ‘Oahu: Nuuanu, Tantalus’.

Lectotype (*L. tantalus*): (Baker, 1963, p. 196), ANSP 108045a (Fig. 9f). H = 3.0 mm. *Paralectotypes*: ANSP 464926 (24 spm). ‘Oahu: southwestern rim of Tantalus bowl, outside’ (Pilsbry & Cooke, 1915 [in 1914–1916], p. 172).

Description: Shell elongate, slightly tapering (Fig. 9e) to wider and shorter (Fig. 9r); parietal lamella large and “strongly flaring outward” (Pilsbry & Cooke, 1915 [in 1914–1916], p. 155). Up to three developing embryos observed with micro-CT (individual in Fig. 8c).

Distribution: Hawaiian Islands (Hawaiʻi, Lanaʻi, Maui, Molokaʻi, Oʻahu).

Ecology: *Lamellidea polygnampta* lives on low vegetation and in moist leaf litter in native Hawaiian forests. Sometimes found with *Freycinetia arborea* (ʻieʻie) and *Pisonia* (pāpala kēpau), and elsewhere with *Toona* sp., *Eugenia*, *Sapindus* canopy. Found on Maui at very low abundance (one individual per site) under *Metrosideros polymorpha* (ʻōhiʻa) canopy with *Dianella*, ferns, and some *Melicope* and ginger. On Lanaʻi, found in damp, shaded area dominated by *Psidium cattleianum* (strawberry guava) and *Casuarina* (ironwood), with some *Dicranopteris linearis* (uluhe) and moss. Some specimens in the BBPM collections were noted as being collected from *Asplenium* spp. ferns. Specimens collected in our surveys were found above 198 meters and as high as 1,179 meters.

Remarks: The species recognized here as *L. polygnampta* includes specimens identified based on morphology as *L. polygnampta polygnampta*, *L. polygnampta kamaloensis*, *L. lanceolata*, and *L. tantalus*. *Lamellidea polygnampta sensu lato* had been previously recorded only from Maui and Molokaʻi (Pilsbry & Cooke 1915 [in 1914–1916]; Cooke & Kondo, 1961). DNA sequenced from one recently collected specimen found at 870 meters in the Makawao Forest Reserve, Maui (PCMB54637), and four historical specimens from Makawao (e.g., Fig. 9c) all belong to the clade identified as *L. polygnampta* (Figs. 1–2). The three specimens from the type locality each had a unique COI haplotype 2.3–3.4% divergent from one another (marked *, Fig. 3c). A historical sample of *L. polygnampta kamaloensis* from Puʻukolekole, Molokaʻi (PCMB50685) is 2.5–3.8% divergent in COI from the Makawao individuals and is nested within the *polygnampta* clade in phylogenetic analyses (Figs 1–2). Samples from the Waiʻanae Mountains of Oʻahu (PCMB54620 and PCMB54621) cluster closely to the historical specimen from Molokaʻi. Delimitation analyses with ASAP indicated that the specimens in the large clade recognized here as *L. polygnampta* could represent between 15 and 27 different species (Fig. 1a), while coalescent-based analyses bPTP and mPTP both recognize this clade as a single species—although with very low support from bPTP (Bayesian support = 0.60). The phylogeny based on nuclear ITS2 sequences supports the mPTP and bPTP delimitations (with the exception of one specimen, PCMB54633, which clusters separately but with low bootstrap support, BS = 75). We follow the bPTP and mPTP analyses in recognizing four *Lamellidea* species in Hawaiʻi: *L. cylindrica*, *L. extincta*, *L. polygnampta*, and *L. peponum* (Fig. 1a). There is little genetic divergence in ITS2 sequences across this group, with the exception of five closely related individuals (clade with PCMB54623, Fig. 1b) collected between 198 and 282 meters elevation (Fig. 4) from the southwest side of the Koʻolau Mountains. Although elevation data is not available for a few specimens, our data indicates most specimens of *L. polygnampta* were collected above 685 meters elevation, and few others were collected from this elevational range.

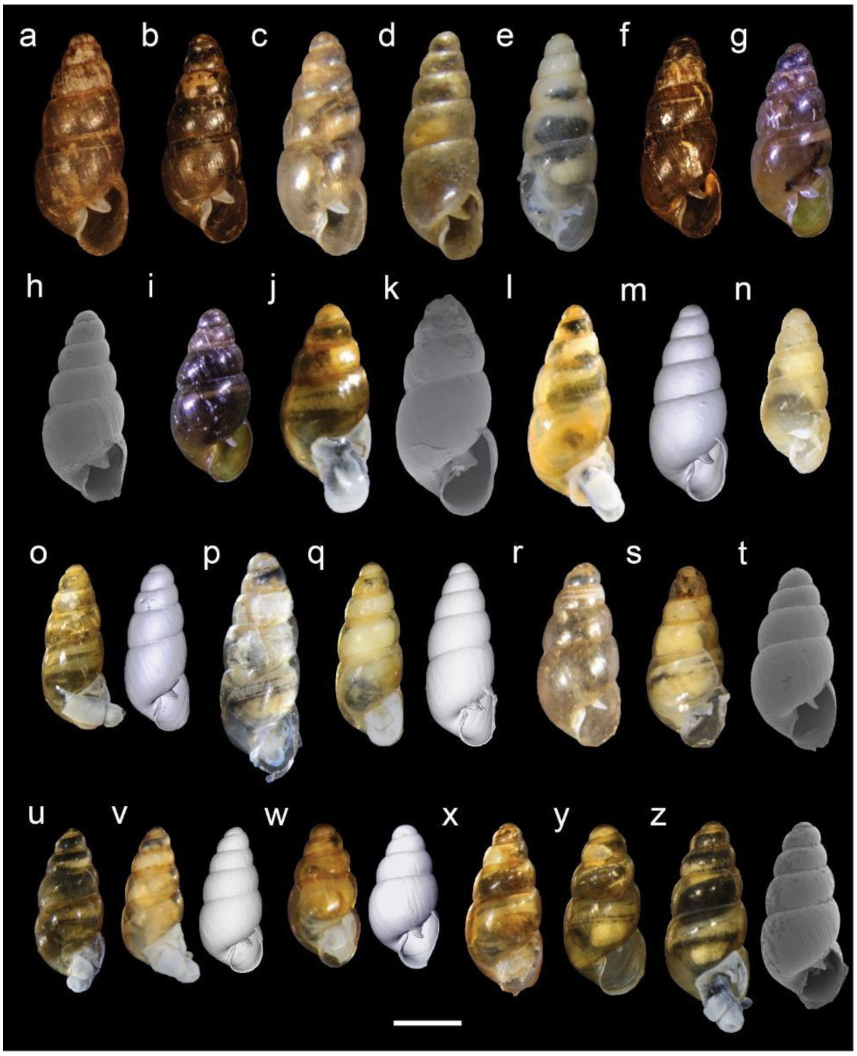


Figure 9. Type material and shells of *Lamellidea polygnampta*

(a) *Tornatellina polygnampta* lectotype ANSP 98049 (b) *Tornatellina polygnampta kamaloensis* lectotype ANSP 109951 Molokaʻi (c) BPBM 170414 Maui (d) *Tornatellina lanceolata* lectotype BPBM 13442 Oʻahu (e) BPBM 288667 Oʻahu (f) *Tornatellina tantalus* lectotype ANSP 108025 Oʻahu (g) BPBM 288716 Oʻahu (h) BPBM 288685 Maui (i) BPBM 288697 Oʻahu (j) BPBM 288701 Oʻahu (k) BPBM 288672 Hawaiʻi (l) BPBM 288702 Oʻahu (m) BPBM 288700 Oʻahu (n) BPBM 288686 Maui (o) BPBM 288694 Maui (p) BPBM 288677 Oʻahu (q) BPBM 288691 Oʻahu (r) BPBM 109670 Maui (s) BPBM 288663 Kauaʻi (t) BPBM 288705 Oʻahu (u) BPBM 288698 Oʻahu (v) BPBM 288690 Oʻahu (w) BPBM 288688 Oʻahu (x) BPBM 288703 Oʻahu (y) BPBM 288665 Kauaʻi (z) BPBM 288682 Maui. Scale bar = 1 mm.

The apparent genetic divergence of this clade from other specimens could be an artifact of the elevational gap in our samples.

The nominal species *L. lanceolata* was originally described from the Koʻolau range of Oʻahu by Pilsbry and Cooke (1915 [in 1914–1916], p. 158), who indicated that it was found "in very damp localities, under dead leaves and twigs." Cooke and Kondo (1961) recorded that the species was also present in the Waiʻanae Mountains of Oʻahu. One specimen collected from native forest in the Waiʻanae Mountains at 840 meters elevation (PCMB54642) is very similar in shell morphology to the lectotype of *L. lanceolata*. A second individual similar in shell shape to *L. lanceolata* (Fig. 9q, PCMB54635) but smaller is not recovered as sister to PCMB54642 in either ASAP delimitation analysis (Fig. 1a) or the multilocus phylogenetic analyses (Fig. 2), supporting the conclusion that similar shell morphology does not necessarily reflect a close phylogenetic relationship. Pilsbry and Cooke (1915 [in 1914–1916]) considered *L. lanceolata* to be more closely related to *L. extincta* (as *T. gracilis*) than other Hawaiian *Lamellidea* based on similarity of their shells, but phylogenetic analyses do not support this.

Pilsbry and Cooke (1915 [in 1914–1916], p. 173) indicated that *L. tantalus* could be found on "lichen growing on damp tree trunks" from Mount Tantalus. *Lamellidea* were collected from Nuʻuanu, Oʻahu at 198 meters elevation less than 2 kilometers northwest of the type locality for this study. One specimen (Fig. 9g, H = 2.9 mm) is similar in shape to the lectotype of *L. tantalus* but with slightly more convex whorls. Closely related specimens are also similar in shape but with less convex whorls (Fig. 9m). The nominal taxon *Lamellidea tantalus* is considered here to be a synonym of *L. polygnampta*.

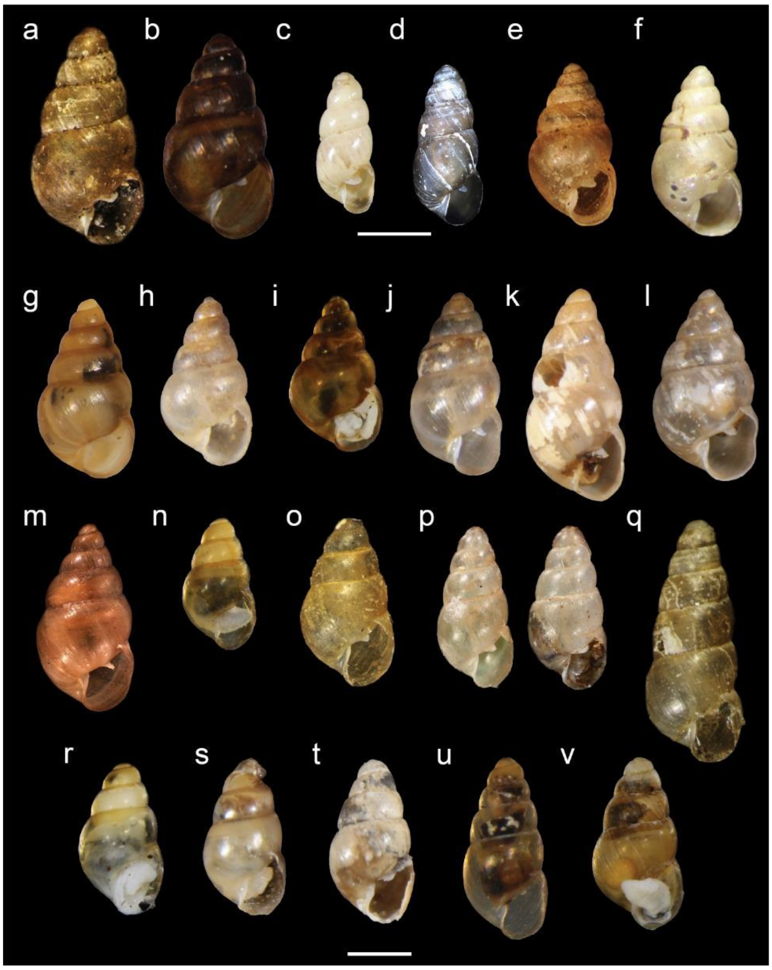


Figure 10. Shells of non-Hawaiian *Lamellidea* species

(a) *Tornelasmias lidgbirdense* Iredale possible holotype AM C.38969 (b) *L. lidgbirdensis* AM C.574969 Lord Howe Island (c) *L. micropleura* Cooke & Kondo holotype BPBM 150531 (d) *L. micropleura* USNM1425107 Moʻorea (e) *L. ogasawarana* Pilsbry & Cooke lectotype ANSP 85760 (f) *L. ogasawarana* BPBM 288653 Ogasawara (g) *L. pusilla* BPBM 288676 Tonga (h) *L. pusilla* BPBM 3353 Society Islands (i) *L. pusilla* BPBM 288693 Niue (j) *L. pusilla* BPBM 212720 Mariana Islands (k) *L. pusilla* BPBM 213592 Mariana Islands (l) *L. pusilla* BPBM 288712 Solomon Islands (m) *L. solomonensis* Dell syntype M.20250 (Museum of New Zealand Te Papa Tongarewa, Creative Commons Attribution 4.0 International Public License, CC-BY 4.0) (n) *Lamellidea* sp. BPBM 288656 Niue (o) *Bulimus jacksonensis* Cox holotype AM C.240 (p) *Tornatellina norfolkensis* Preston syntypes SMF 164950 (q) *L. capricorni* Iredale syntype AM C.107410 (r) *L. novoseelandica* BPBM 288661 New Zealand (s) *L. novoseelandica* AM C.574950 Lord Howe Island (t) *L. novoseelandica* AM C.559477 New South Wales (u) *L. novoseelandica* BPBM 288659 Chatham Island (v) *L. novoseelandica* AM C.395538.001 Norfolk Island. Scale bars = 1 mm (part c–d has a separate scale bar from the rest of the figure).

3.4 Non-Hawaiian species

Lamellidea lidgbirdensis *(Iredale, 1944) (Figs. 10a–10b)*

Holotype and paratypes: AM C.38969 (3 spm). H = 3.4 mm, *possible holotype* (Fig. 10a). *Paratypes*: H = 3.6 mm. ‘Black Face of Mt Lidgbird, and elsewhere in the heights’ [Lord Howe Island] (Iredale, 1944, p. 309).

Ecology: Leaf litter in open forest and tall forest (Smith, 1992); rainforest, rock faces, in leaf litter, on palms (AM C.38969) at high elevation (573 m).

Remarks: Iredale (1944) recorded this putative endemic species of *Tornelasmias* [= *Lamellidea*] from Lord Howe Island and indicated that “the type” was 3.25 mm in height and 1.75 mm in width. Three specimens in AM C.38969 are currently regarded as syntypes, but a specimen matching Iredale’s measurement should be considered the holotype by original designation (ICZN Code Art. 73.1.1). The imaged specimen is slightly larger than Iredale’s measurement and is considered here to possibly be the holotype (Fig. 10a). *Tornelasmias lidgbirdense* was described as having a more broadly conical shell and living at higher elevations than *T. capricorni* and *Tornatellina inconspicuum*. One specimen from Lord Howe Island (Fig. 10b) yielded a short COI sequence and a 28S sequence that differed substantially from other samples in the *novoseelandica* clade (5.8–7.5% in COI, 0.6% in 28S). We provisionally interpret it as representing *L. lidgbirdensis*, but additional samples are needed to better resolve the relationships among the Lord Howe Island Pacificellinae.

Lamellidea micropleura *Cooke & Kondo, 1961 (Figs. 10c–10d)*

Holotype: BPBM 150531 (Fig. 10c). *Paratypes*: BPBM 150532 (5 spm), BPBM 150533 (3 spm), and BPBM 150534 (9 spm). ‘Society Islands: Moorea, Faatoai Valley’ (Cooke & Kondo, 1961, p. 194).

Distribution: Moʻorea, French Polynesia.

Ecology: Cooke & Kondo (1961, p. 194) noted that *L. micropleura* was found "under loose bark or lichens growing on trees".

Remarks: Lamellidea micropleura differs from *L. peponum* in having a smaller and more slender shell. These two species are locally sympatric in French Polynesia but occupy different niches.

Lamellidea novoseelandica *(Küster, 1852)* *(Figs. 10o–10v)*

Tornatellina novoseelandica Küster, 1852, p. 149, pl. 18, figs. 10, 11.

Bulimus jacksonensis Cox, 1864, p. 25. **New synonym.**

Tornatellina inconspicua Brazier, 1872, p. 619. **New synonym.**

Tornatellina duplicilamellata Preston, 1913, p. 537. **New synonym.**

Tornatellina norfolkensis Preston, 1913, p. 536. **New synonym.**

Tornatellina norfolkensis moohuensis Preston, 1913, p. 537. **New synonym.**

Tornatellina norfolkensis nepeanensis Preston, 1913, p. 537. **New synonym.**

Tornelasmias capricorni Iredale, 1944, p. 308, pl. 18, figs. 6, 6a. **New synonym.**

Type (*T. novoseelandica*): Whereabouts not known, probably lost or destroyed (Brook & Ablett, 2019). 'Neuseeland' (Küster 1852, p. 150).

OTHER TYPE MATERIAL

Syntype (*B. jacksonensis*): AM C.240. 'Darling Point, Port Jackson' [Australia] (Cox 1864, p. 25).

Type (*T. inconspicua*): Formerly in AM, whereabouts not known, presumed lost or destroyed (Smith, 1992, p. 87). 'Lord Howe's Is.' (Brazier 1872, p. 619).

Syntypes (*T. duplicilamellata*): AM C.37148 (2 spm). 'Nepean Island' [Norfolk Island] (Preston 1913, p. 537).

Syntypes (*T. norfolkensis norfolkensis*): AM C.37154 (2 spm), NHMUK 1911.8.22.89-90 (2 spm), NHMUK 1913.7.31.320-322 (3 spm), SMF 164950/2 (2 spm) (Fig. 10p). 'Ball's Bay, Norfolk Island' (Preston 1913, p. 536).

Syntypes (*T. norfolkensis moohuensis*): AM C.37172 (3 spm), AM C.115518 (5 spm). 'Moohu Stone, a small islet off the coast of Norfolk Island' (Preston 1913, p. 537).

Type (*T. norfolkensis nepeanensis*): Whereabouts not known, probably lost or destroyed (Smith, 1992, p. 88). 'Nepean Island' [Norfolk Island] (Preston 1913, p. 537).

Syntype (*T. capricorni*): AM C.107410 (1 spm). 'Goat (or Rabbit) Island' [Lord Howe Island] (Iredale, 1944, p. 308).

Description: Shell oblong; parietal lamella small.

Distribution: New Zealand (North Island, northern South Island, Three Kings Islands, Chatham Islands), eastern Australia from Queensland to Flinders Island, Lord Howe Island, Norfolk Island.

Ecology: Lamellidea novoseelandica is present in a wide range of habitats in New Zealand, from the coast to altitudes of several hundred meters, in native grassland, shrubland, and tall forest. It lives on the ground in leaf litter and arboreally on shrubs, palms, trees, and in litter suspended in vines and epiphytes (e.g., Brook, 1999, 2002; Brook & Goulstone, 1999; Climo, 1973). On Lord Howe Island, *L. novoseelandica* has been recorded from coastal tussockland (PCMB54667), open scrub and woodland (Smith, 1992 – as *Tornatellinops inconspicua*), sclerophyll forest (PCMB51690), and *Cleistocalyx-Chionanthus* forest (PCMB51686). On Norfolk Island, it has been recorded from scrub and woodland (Smith, 1992), while the specimen analyzed here was collected from a small sand quarry with white oak. On mainland Australia, *L. novoseelandica* inhabits coastal grassland, scrub, and tall, closed forest (Smith, 1992; Stanisic et al., 2018 – as *Tornatellinops jacksonensis*). All specimens sequenced in this study were found at low elevation, from sea level to 130 meters elevation.

Remarks: *Lamellidea novoseelandica* had previously been assigned to *Tornatellinops*, but phylogenetic analyses place the species within the clade of *Lamellidea* species. This placement corroborates Climo's (1973) taxonomic treatment based on anatomical characters.

Lamellidea novoseelandica was previously thought to be restricted to New Zealand, including Three Kings Islands, North Island, northern South Island, and Chatham Islands (Brook & Ablett, 2019). However, in our phylogenetic analyses, specimens of *L. novoseelandica* from New Zealand clustered with samples from southeastern Australia, Lord Howe Island, and Norfolk Island (Fig. 1), indicating that this species has a trans-Tasman distribution. Australian Pacificellinae have been described under several different species and subspecies names (see Cooke & Kondo, 1961; Smith, 1992) but Stanisic et al. (2010, p. 534, 2018, p. 554) synonymized *Tornatellina inconspicua* Brazier, 1872; *T. duplicilamellata* Preston, 1913; *T. norfolkensis* Preston, 1913; *T. norfolkensis moohuensis* Preston, 1913; and *T. norfolkensis nepeanensis* Preston, 1913 with *Tornatellinops jacksonensis* (Cox, 1864). Here, we treat all of these taxa as junior synonyms of *L. novoseelandica* (Küster, 1852). We infer the type specimen of *Tornatellinops jacksonensis*, AM C.240, to be a syntype following Recommendation 73F of the ICZN Code. Smith (1992, p. 87) previously identified the specimen in this lot as the holotype of *T. jacksonensis*. However, Cox's description indicates that the species is "imperforate or obsolete" ["imperforatâ vel obsoletè"], which implies that it was based on more than one specimen. This is supported by the fact that the specimen in AM C.240 is only ~2.6 mm, whereas the measurements provided by Cox indicate 0.14 inches, approximately 3.5 mm. Smith did not explicitly indicate that he was selecting a specimen from the type series to serve as a name-bearing type, thus, according to the ICZN Code, Art. 74.5, his use of the term "holotype" is not a valid lectotype designation.

Cooke & Kondo (1961, p. 172) suggested that *Tornelasmias capricorni*, which was described from material collected on an islet in the lagoon at Lord Howe Island, may belong to *Lamellidea*. Based on our DNA sequences of *Lamellidea* from Lord Howe Island, this species is probably also a junior synonym of *L. novoseelandica*. *Tornatellina iredalei* Pilsbry & Cooke, 1915 [in 1914–1916], described from Raoul Island, Kermadec Islands is another likely synonym, but genetic data from these islands are required to evaluate this possibility.

Lamellidea novoseelandica is recovered as monophyletic in multilocus phylogenetic analyses (Fig. 2), but in analyses of COI sequences it is paraphyletic with respect to *L. lidgbirdensis* from Lord Howe Island (Fig. 1a). It is geographically structured into two allopatric subclades, the first comprised of individuals from northern North Island (Fig. 10r), Three Kings Islands, Norfolk Island (Fig. 10v), Lord Howe Island (Fig. 10s), and New South Wales (Fig. 10t), and the second from northern South Island and Chatham Islands (Fig. 10u). These two subclades are consistently recognized as distinct species in species delimitation analyses (Fig. 1a). The genetic divergence between these two clusters is 3.6–4.7% in COI, comparable to that observed between *L. peponum* and *L. micropleura* (4.3-5.2%). Preliminary qualitative observations suggest that shell shape is fairly uniform within some local populations but variable in others. *Lamellidea novoseelandica* is provisionally interpreted here as a morphologically variable species, with shell shape ranging from slender (e.g., typical of *norfolkensis,* Fig. 10p, and *capricorni*, Fig. 10q) to more broadly conical (e.g., typical of *jacksonensis,* Fig. 10o). Further work is required to evaluate if the two clades identified in our analyses merit recognition as valid species.

Lamellidea ogasawarana *(Pilsbry & Cooke, 1915) (Figs. 10e–10f)*

Lectotype: ANSP 85760. *Paralectotypes*: ANSP 453111 (2 spm). Bonin Islands (Minami-jima', Ogasawara-jima).

Remarks: The two specimens included in our analyses (Fig. 10f) are from the Ogasawara Islands (PCMB54660 and PCMB54661), and both have a smaller parietal lamella than the lectotype (Baker 1963, p. 196) of *L. ogasawarana* (Fig. 10e) but are otherwise similar. Cooke & Kondo (1961, p. 184) considered *L. ogasawarana* to be closely related to four other western Pacific species of *Lamellidea* (viz., *L. biplicata* (Pilsbry, 1902), *L. subcylindrica* (Möllendorff & Quadras, 1894), *L. microstoma* (Möllendorff & Quadras, 1894), *L. solomonensis* Dell, 1955) and *L. pusilla*, but our analyses indicate it is more closely related to *L. peponum* and *L. micropleura* (Fig. 2).

Lamellidea pusilla *(Gould, 1847) (Figs. 10g–10m)*

Syntype(s): USNM 5492; reported missing by Pilsbry and Cooke (1914–1916, p. 176) and Johnson (1964, p. 136) and not found during a search of the USNM collection in 2019. 'Matea Island' (Gould, 1847, p. 197), 'Metia Island' (Gould, 1852), 'Makatea Island, Tuamotu Islands' according to Pilsbry and Cooke (1915 [in 1914–1916], p. 176).

Description: Shell strongly tapered, oblong; parietal lamella small to moderate.

Ecology: In the Cook Islands, *L. pusilla* is present in coastal shrubland and forest, living on the ground among fallen leaves and dead wood, and on ferns and shrubs (Brook, 2010). Specimens analyzed from Tonga and Niue were collected at low elevation (between 12 and 20 meters); elevation data was not available for the other specimens.

Remarks: Cooke & Kondo (1961, p. 185) interpreted this species as having a broad distribution in the Pacific, from Marianas and Caroline Islands east to French Polynesia, which they attributed in large part to anthropogenic dispersal. *Lamellidea pusilla* is a morphologically variable species and has been described under many different names, as indicated in synonymies by Cooke & Kondo (1961, pp. 184–185) and Kondo (1975, p. 114). Our phylogenetic analyses include historical museum specimens of *pusilla* from Mariana Islands, Solomon Islands, the Society Islands, and recently collected material from Tonga and Niue. The mPTP species delimitation analysis recognizes all specimens of *L. pusilla* in our analyses as a single species (Fig. 1a), while the other species delimitation analyses suggest that these specimens may represent between three (ASAP) and five species (bPTP) (Fig. 1). Although mitochondrial sequence data from *L. pusilla* are characterized by high genetic divergence between individuals (up to 10.3% in COI), the sampling of this species is limited across the Pacific, which would be expected to contribute to over-splitting by species delimitation analyses.

One subclade of *L. pusilla* delimited as a species by ASAP (#9) is comprised of individuals from Tonga (Fig. 10g), the Society Islands (Fig. 10h), and Saipan, Mariana Islands (10j). The individual from Tonga and the historic specimen collected by A. Garrett from the Society Islands have a similarly tapered shell (H = 2.7–3.0 mm, Figs 10g, 10h). A smaller specimen from Niue is also similarly tapered (H = 2.6 mm, Fig. 10i). The specimens from Tinian, Mariana Islands and a historical specimen from the Solomon Islands (Figs. 10k, 10l) cluster together in phylogenetic analyses. The specimen from the Solomon Islands has a slightly broader shell than other specimens in the *L. pusilla* clade and is similar in shape to a syntype of *L. solomonensis* (Fig. 10m), which Kondo (1975) treated as a junior synonym of *L. pusilla*. Cooke & Kondo (1961, p. 188) hypothesized that *L. pusilla* originated in the Western Pacific and was dispersed eastwards by humans, but additional genomic data are needed to investigate patterns of dispersal.

Lamellidea *sp. (Fig. 10n)*

Description: Shell elongate, slender; parietal lamella small.

Distribution: Niue.

Ecology: Leaf litter in coastal forest.

Remarks: The single specimen of this species in our dataset is a juvenile (H = 2.2 mm, Fig. 10n) with a relatively slender spire, similar in shape to *L. novoseelandica* and *L. peponum*. It was identified in phylogenetic analyses as a divergent lineage sister to *L. novoseelandica* (BS 93, Fig. 1), although this was not recovered in the multilocus analysis (Fig. 2). Further genomic data are needed to determine if this taxon is restricted to Niue or more widely distributed in SW Polynesia.

4 DISCUSSION

4.1 Species delimitation

Molecular data are critical for delimiting species in an integrative framework; for these Pacific Island land snails, phylogenetic trees, species delimitation analyses, and haplotype networks were analyzed and considered in light of shell morphology and geographic data in order to revise the taxonomy. The molecular delimitation methods employed seek to identify a transition between intraspecific and interspecific genetic divergence; however, many factors can influence the results of these analyses, including dispersal ability, life history, and taxon sampling. Genetic diversity within a species is influenced by adaptation to local environmental conditions and genetic drift within and between populations, while gene flow may act to inhibit local adaptation and homogenize genetic diversity among populations (Slatkin, 1987). In terrestrial invertebrates with limited means for active dispersal, there is expected to be relatively high genetic divergence between populations, and it can be difficult to differentiate a group of closely related species from genetic divergence among allopatric populations of the same species, particularly with single locus molecular data (Sauer & Hausdorf, 2012). Delimitating species with low mobility also requires sampling of genetic diversity across their geographic distributions, as incomplete sampling can lead to over-splitting (Mason et al., 2020; Phillips et al., 2019; Zwickl & Hillis, 2002).

Sex ratios and mode of reproduction in land snails may also contribute to unusual patterns of gene flow and diversification. In gonochoristic taxa, random mating should lead to a unimodal distribution of pairwise genetic distances in the absence of selection on a particular locus, though population subdivision can influence this (Marjoram & Donnelly, 1994). Deviations from random mating due to asexual reproduction or self-fertilization could lead to population subdivision and a multimodal distribution of pairwise differences within a single species, contributing to misleading results from molecular delimitation methods. Stylommatophoran gastropods generally reproduce sexually but are hermaphroditic, and a small number of families are known to be capable of self-fertilization (Heller, 2001). Lab studies of several species of Pacific Island land snails in the Achatinellidae and Partulidae indicate that these species may reproduce by self-fertilization (Kobayashi & Hadfield, 1996; Murray & Clarke, 1966; M. R. Price et al., 2015), and comparative anatomy has shown that *Lamellidea* is one of two genera of Pacific Island land snails with an unusual proportion of aphallic individuals (Cooke & Kondo, 1961). As many as four out of five adult *Lamellidea* snails have been found to be aphallic in some species (Cooke & Kondo, 1961, p. 196), and these snails may either reproduce sexually with snails with a phallus or self-fertilize. Species delimitation analyses of snails that are facultatively self-fertilizing have produced conflicting results, providing support to the theory that this life history trait may contribute to patterns of genetic divergence that result in over-splitting by some molecular delimitation analyses (Prévot et al., 2013).

Species delimitation analyses differed widely in the number of pacificelline species estimated, with between 6 and 42 species of *Lamellidea* and *Pacificella* delimited from the Hawaiian Islands (Fig. 1a), and several factors have likely contributed to this. In gastropods, high intraspecific genetic distances in mitochondrial DNA (greater than 5%) are known from diverse terrestrial taxa and some marine groups and are sometimes attributed to an elevated rate of mitochondrial evolution (Fourdrilis et al., 2018; Haase et al., 2003; Hayashi & Chiba, 2000; Pinceel et al., 2005; Thomaz et al., 1996). In stylommatophoran snails like pacificellines, there is also a large overlap between genetic variation within species and divergence between species, which complicates the identification of species based on DNA barcodes (Davison et al., 2009). Delimitation analyses of terrestrial gastropod taxa should therefore be interpreted cautiously due to the likelihood of over-splitting taxa, including distance-based methods, like ABGD and ASAP, and coalescent methods, like GMYC (Dellicour & Flot, 2018; Pentinsaari et al., 2017). Over-splitting is also likely to be a challenge for the delimitation of pacificellines because Hawaiian gastropods have undergone sharp declines in abundance and extinction of species over the last several decades, and it is likely that recent surveys have sampled a small fraction of the previous genetic diversity. In these circumstances, mPTP analysis is possibly the best suited for delimiting pacificelline species as the multi-rate PTP model allows significant variation in genetic diversity between closely related species and is less impacted by sampling bias (Kapli et al., 2017).

Shell morphology can provide characters useful for distinguishing gastropod species as part of an integrative taxonomic approach (Horsáková et al., 2020; Pholyotha et al., 2020; Sawada et al., 2021), but high intraspecific variation in shell morphology has also been observed in some island gastropod taxa, evidence that over-reliance on shell characters can lead to taxonomic over-splitting (M. S. Johnson & Stankowski, 2018; Köhler et al., 2020; Stankowski, 2011). The unornamented and variable shells of *Lamellidea* and *Pacificella* species were previously considered to represent eight *Lamellidea* species in the Hawaiian Islands (Pilsbry & Cooke 1915 [in 1914–1916]; Cooke & Kondo, 1961), but it remained difficult to identify taxa to species level based on high intraspecific variation. The lack of diagnostic shell differences coupled with the high variance in the number of species delimited with molecular data makes it difficult to define species boundaries in pacificellines. Although genetic divergence in mitochondrial sequences is high and could be delimited as 42 or more *Lamellidea* species in Hawaiʻi, nuclear ITS2 sequences did not differentiate the multitude of Hawaiian *Lamellidea* lineages delimited by ASAP. The nuclear ITS2 locus is a fast-evolving locus that has been used to distinguish between closely related species of diverse land snails (Garzia et al., 2021; Prévot et al., 2013; Razkin et al., 2017; Zając et al., 2020), but the phylogenetic tree estimated from pacificelline ITS2 sequences supported a small number of clades. Of the taxa sampled from Hawaiʻi, four clades were supported, recognized here as *Lamellidea cylindrica, L. polygnampta*, *L.*

peponum, and *P. variabilis* (ITS2 sequences could not be obtained for *L. extincta* or *P. baldwini*). Even with indel coding to utilize insertions/deletions that might distinguish closely related species, there was little support for the genetic clusters within *L. polygnampta* that were recovered with the mitochondrial data (Fig. 1). Discordance between the clustering of mitochondrial and nuclear loci within *L. polygnampta* could be interpreted either as the result of gene flow between populations or incomplete lineage sorting between recently diverged taxa (Funk & Omland, 2003), but these two competing hypotheses could not be resolved with the data available.

Integrating mitochondrial and nuclear DNA sequences with morphological analyses is necessary for distinguishing complexes of morphologically similar species, but it can still be difficult to draw conclusions from these data. The bPTP and mPTP analyses agreed on the delimitation of most taxa but differed in their delimitation of *L. extincta*, *L. pusilla*, and the *Pacificella* species. We recognize *P. baldwini* as distributed from the main Hawaiian Islands to Kure and Johnston Islands based on the mPTP analysis but acknowledge this is based on limited molecular data and should be investigated further. Species delimitation analyses also differed in the delimitation of *Pacificella variabilis*; mPTP suggests that three specimens from Tahiti and Oʻahu belong to *P. variabilis*, while these three specimens were each considered to represent different species by ASAP and bPTP. *Pacificella baldwini*, *P. variabilis*, *L. extincta*, and *L. pusilla* are all characterized by large geographic distances between populations, and the conservative estimation of 13 pacificelline species by mPTP analysis is supported by the current data. However, the delimitation of species in this study is based primarily on analysis of mitochondrial DNA barcodes; moving forward, additional loci should be added from the nuclear genome, preferably genomic data that can better resolve introgression and population structure. In the case of Pacific Island land snails that are declining and slowly disappearing, analysis of historical specimens can help in delimiting species that would otherwise be represented by few samples in molecular datasets.

4.2 Diversification in Hawaiʻi

Many of the plants and animals on the main Hawaiian Islands are hypothesized to have originated in the last several million years after the formation of Kauaʻi (J. P. Price & Clague, 2002). The island of Oʻahu is geologically young, formed by three volcanos between 2.6 to 3.5 million years ago (Sinton et al., 2014), and is home to the only pacificelline species that appears restricted to a single island, *L. cylindrica*. The volcanic islands of Kauaʻi, which formed 4.7 Ma, and the northwestern Hawaiian Islands, which formed between 7.3 and 29.8 million years ago (J. P. Price & Clague, 2002), are all older than Oʻahu, but several other groups of Hawaiian land snails also reach their greatest diversity on Oʻahu. These include the Achatinellinae (Cowie & Holland, 2008), *Auriculella* (Pilsbry & Cooke, 1912–1914; Yeung et al., 2020), and the Amastridae (Hyatt & Pilsbry, 1910–1911; Régnier et al., 2015), and together this suggests that the higher diversity on the island of Oʻahu is a recurring pattern among land snails and unlikely to be an artifact of sampling effort. Of course, patterns of diversity in Hawaiian land snail taxa may differ due to the timing of colonization and dispersal events (Cowie, 1995).

The topographic complexity of the Hawaiian Islands has contributed to allopatric speciation of many Hawaiian taxa, including tree snails (Hyatt & Pilsbry, 1910–1911; J. P. Price & Clague, 2002). However, pacificellines differ ecologically from the achatinelline tree snails that do not frequently disperse far from their colony in that the minute pacificellines are often ground-dwelling and may be more easily dispersed by wind and heavy rains on steep mountain slopes. In contrast to the high diversity of tree snail species in the Hawaiian Islands, which are thought to be the result of non-adaptive radiation among allopatric populations (Gulick, 1905; Rundell, 2011), the genetic data analyzed here do not indicate clustering of pacificellines by locality, suggesting dispersal of Pacificellinae snails across mountain ranges and between islands or, conversely, the result of a formerly contiguous distribution. The mosaic of genetic diversity across islands in the Pacificellinae contrasts with the expectation for snails to be characterized by small geographic ranges and to have diverged from neighbors on nearby mountain ridges and valleys due to isolation. Instead, the native *Lamellidea* species appear to differ in elevational range. *Lamellidea extincta* is a lowland species distributed across coral atolls of the northwestern Hawaiian Islands to the main islands, *L. cylindrica* is present at low to moderate elevations from 10 to 710 meters, and *L. polygnampta* is a high elevation species that occurs across a broad elevational gradient (mean 870 meters, Fig. 4c).

4.3 Dispersal across the Pacific

Lamellidea and *Pacificella* are both widely distributed across the islands of the Pacific, which contrasts to the endemicity of the larger achatinellid genera, *Achatinella*, *Auriculella*, and *Partulina* (Cowie et al., 1995; Pilsbry & Cooke, 1912–1914), and some smaller achatinellid genera like *Tornatellaria* and *Philopoa* (Pilsbry & Cooke 1915 [in 1914–1916]; Cooke & Kondo, 1961). The presence of endemic species of *Lamellidea* and *Pacificella* on remote oceanic islands indicates that there has been a long history of dispersal of these taxa within the Pacific, predating the arrival of humans in Oceania. Dispersal of Pacificellinae propagules to oceanic islands, and successful establishment of island populations, were presumably relatively rare, stochastic events prior to human voyaging and settlement in the Pacific. The means by which Pacificellinae could have dispersed between islands may have included transport in the digestive tract of or attached to migratory birds (e.g., Kawakami et al., 2008; Wada et al., 2011/2012) or by wind, especially with storms and hurricanes that occur regularly in the Pacific and periodically pass through the Hawaiian Islands (Cowie & Holland, 2006; Gillespie et al., 2012; Vagvolgyi, 1975; Visher, 1925).

The Pacificellinae includes a few species that have exceptionally wide distributions among island groups in the Pacific, which have been attributed in part to anthropogenic dispersal and is supported by archaeological evidence (e.g., Cooke & Kondo, 1961; Dixon et al., 1997; Preece, 1998). Two of these species, *Lamellidea peponum*, and *Pacificella variabilis*, are present in Hawai‘i and are similar morphologically to species endemic to Hawai‘i. Both *Lamellidea peponum* (as *L. oblonga* or *L. peponum*) and *P. variabilis* have not been identified from Pleistocene or early- to mid- Holocene fossil beds (Cooke & Kondo, 1961, p. 202; C. Christensen, pers. comm.). Phylogenetic analyses of DNA sequences of *P. variabilis* suggest there are multiple source populations for the individuals in the Hawaiian Islands, as specimens from O‘ahu are closely related to specimens from the Cook Islands, while the specimens from Kaua‘i are related to specimens from French Polynesia. It is not yet known if *P. variabilis* is established on Kaua‘i or Hawaiian Islands other than O‘ahu, but many of the snail species introduced to Hawai‘i have successfully colonized multiple islands (Cowie, 1997). Genetic divergence is quite low between the Hawaiian specimens of *L. peponum* and a specimen from Aitutaki, Cook Islands, but this species is known from many other island groups that remain unsampled, so it is too soon to assess intraspecific diversity in this species or form hypotheses on the source population(s). Resolving the complex history of dispersal and diversification of the pacificellines across islands of the Pacific will require genomic data and broader sampling across Polynesia.

While the mPTP delimitation analysis supports previous hypotheses of the widely distributed *Lamellidea* species *L. peponum*, *L. extincta*, *L. pusilla*, and *P. variabilis*, all species delimitation analyses recognized two species of *L. novoseelandica*. Current data suggest that these two groups are allopatric, with a widely distributed northern group encompassing northern New Zealand, Three Kings Island, Norfolk Island, Lord Howe Island, and New South Wales, Australia, which are differentiated genetically from a southern group from southern New Zealand and the Chatham Islands. The broad distribution of *L. novoseelandica* in New Zealand is not likely to be an artifact of anthropogenic transport as fossil evidence indicates a wide distribution of *L. novoseelandica* in the New Zealand region prior to human settlement (Brook, unpublished data). Likewise, Cooke and Kondo (1960, p. 211) noted that there are no records of Polynesian settlement on Wake Atoll that would explain the dispersal of *L. extincta* to the distant island.

The wide distribution of the pacificellines in the Pacific may have been aided in part by their mode of reproduction. Studies of achatinellid reproduction indicate that achatinellids are self-compatible and may reproduce by self-fertilization (Kobayashi & Hadfield, 1996; M. R. Price et al., 2015). While reproduction has not been studied in pacificellines specifically, the internal anatomy of pacificellines indicates that aphallic individuals of *L. peponum* often have developing embryos within their reproductive tract (Goulding & Slapcinsky, unpublished data). In addition, single embryos were also observed in aphallic individuals of the high elevation species *L. polygnampta* (as *L. tantalus,* Cooke & Kondo, 1961), and, given the proportion of aphallic individuals observed by those authors, we hypothesize that self-fertilization may be occurring in these *Lamellidea* species.

4.4 Conservation

Historical collections indicate that Pacificellinae species were abundant in Hawaiian forests as recently as the beginning of the twentieth century. In contrast, recent surveys across the main islands have recovered few individuals of some species and none of others (Yeung & Hayes, 2018) and indicate that the abundance of *Lamellidea* and *Pacificella* species is lower than many other achatinellid microsnails. The distributions of Hawaiian snails have been fragmented by habitat loss since western contact, but the direct and indirect impacts of introduced species are thought to have had a larger role in the recent declines in Pacific Island land snails (Gerlach et al., 2020). Currently, all achatinellid microsnails are regarded as data deficient in the IUCN Red List (IUCN, 2021), and only species in the Achatinellinae are recognized as endangered under the US Endangered Species Act (USFWS, 1981, 1993). Here, we show that no individuals of *Lamellidea extincta* and *Pacificella baldwini* have been found during land snail surveys carried out by the authors and local collaborators in the Hawaiian Islands. Collections from the Bishop Museum suggest the last time these species were collected alive in the main Hawaiian Islands was the 1940s; it is likely that these species are now critically endangered or possibly extinct. The low abundance of endemic *Lamellidea* species also suggests that Hawaiian Pacificellinae species are in decline and may be threatened with extinction in the near future.

This study of the Pacificellinae illustrates the value that molecular data has in investigations of snails with large geographic distributions and few diagnostic morphological characters. However, despite intense sampling effort, precipitous declines in diversity and abundance of Pacific Island land snails have made it increasingly difficult to obtain the samples necessary for modern systematic studies, particularly for low elevation species that have been disproportionately impacted by human mediated threats. It is only through preserved natural history collections that two pacificelline species absent in modern surveys could be incorporated into a molecular phylogenetic framework. Historical specimens were also invaluable for broadening the geographic sampling of this study to include type localities and distant atolls and for expanding the number of taxa analyzed to better understand genetic divergence between species (Goulding et al., 2021). There remain many groups of Pacific Island microsnails in which diversity remains poorly understood, and, consequently, these snails are not being considered in conservation management. Additional integrative studies, especially those using museum specimens, pairing molecular analyses with data on the biology and morphology of these snails are critically needed to broadly assess microsnail biodiversity across the Pacific.

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Data Availability

All DNA sequence data and analyses from this study are publicly available. GenBank accession numbers are provided in Table 1 and alignments and phylogenetic trees can be downloaded from TreeBASE: http://purl.org/phylo/treebase/phylows/study/TB2:S29512. Shell images and 3D micro-CT models were uploaded to the online database MorphoBank: http://morphobank.org/permalink/?P565.

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Supplementary Materials

Supplementary Figure 1. Phylogenetic tree based on partitioned maximum likelihood analysis in IQ-Tree. Five partitions analyzed: COI (1st and 2nd codon position, 3rd codon position), 16S (alignment modified by Gblocks), ITS2 and 28S. Numbers at the nodes indicate Bootstrap support. The names of Hawaiian pacificelline species are indicated in bold.

Supplementary Figure 2. Phylogenetic tree based on partitioned Bayesian analysis in MrBayes. Five partitions analyzed: COI (1st and 2nd codon position, 3rd codon position), 16S (alignment modified by Gblocks), ITS2 and 28S. Numbers at the nodes indicate posterior probabilities. The names of Hawaiian pacificelline species are indicated in bold.

Supplementary Figure 3. Micro-CT 3D interactive images of *Hawaiian Lamellidea* species, including apertural and longitudinal sectional views showing the length of the parietal lamella and developing embryos (a) *Lamellidea peponum* PCMB54658 (BPBM 287046) (b) *L. cylindrica* PCMB54648 (BPBM 288696) (c) *L. polygnampta* PCMB54617 (BPBM 288681) (d) *L. polygnampta* PCMB54623 (BPBM 288700) (e) *L. polygnampta* PCMB54628 (BPBM 288698) (f) *L. polygnampta* PCMB54629 (BPBM 288703) (g) *L. polygnampta* PCMB54625 (BPBM 288694) (h) *L. polygnampta* PCMB54635 (BPBM 288691). Micro-CT images of additional specimens are available at http://morphobank.org/permalink/?P565.

Supplementary Table 1. Intraspecific and interspecific uncorrected genetic divergence (percentage) in COI of *Lamellidea* and *Pacificella* species.

Supplementary Table 2. Number of radular teeth per row in select *Lamellidea* and *Pacificella* species.

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