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Description of *Laoma ordishi* new species (Eupulmonata: Punctidae) and reinstatement of *Laoma nerissa* (Hutton, 1883)

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Abstract
Laoma s.str., based on *Laoma leimonias* (Gray, 1850), also includes *L. marina* (Hutton, 1883), *L. ordishi* Climo n. sp., *L. labyrinthica* Powell, 1948 and *L. nerissa* (Hutton, 1883), which is reinstated as a valid species. Recently collected material of these *Laoma* spp. from a wide spread of localities in New Zealand shows that reabsorption of apertural lamellae during growth does not change their configuration in the manner proposed by Suter (1891: 283–285). All species discussed here are endemic to New Zealand. They overlap tightly in their distribution but are often allopatric at local scale, around Auckland–Waitemata–Hauraki Gulf, North Island, while elsewhere they are geographically well-separated. The naturally uncommon *L. labyrinthica* (Three Kings Islands) is the only species of conservation concern in this group.

Keywords
Laominae; New Zealand; terrestrial gastropods; taxonomy; new species.

Registration ID: *Laoma nerissa*
LSID urn:lsid:zoobank.org:pub:22B84676-5098-43C7-85E9-B3F6D9D14078

INTRODUCTION

Hutton described *Endodonta marina* and *E. nerissa* in 1883 and 1884, in the *New Zealand Journal of Science* and in the *Transactions and Proceedings of the New Zealand Institute* respectively (Hutton 1884a, b). Suter (1891: 271) transferred both species to *Phrixgnathus (Laoma)* based on 'spiral lamellae and teeth in the aperture.' In the subsequent mention of these species on p. 283, they were referred to as '*Laoma marina* Hutt. and *Laoma nerissa* Hutt.'

In his original description of *E. nerissa* Hutton clearly states: '…a columellar plait and six parietal plaits, three of which are on the basal margin' (Hutton 1883: 476) and for *E. marina* '… a columellar plait, and two parietal plaits, none of which are on the basal margin' (Hutton 1883: 476). However, eight years later, Suter (1891) synonymised *Laoma nerissa* with *L. marina*, based on a detailed analysis of their apertural lamellae and other shell features. He concluded that *L. nerissa* was a juvenile form of *L. marina* (Fig. 1): 'All my observations lead me to the conclusion that in the young shells all the seven plaits are developed, but are reabsorbed later on in such a way that 7 first disappears, followed by 2, 5, 6, thus leaving for the adult shell the plaits 1, 3, 4 only. I am of opinion that all these facts taken together show clearly that *L. marina* and *L. nerissa* are but one species' (Suter 1891: 284). He also said 'The name which has to be retained is *Laoma marina* Hutt., being that of the adult shell' and provided a diagnosis of *Laoma marina* Hutt. (1883) (=*Laoma nerissa* Hutt., 1883).

Our examination of more recently collected material from a wider spread of localities shows that while apertural lamellae are reabsorbed during growth, this does not change their configuration in the manner proposed by Suter (1891). A comparison between *L. nerissa* and *L. marina*

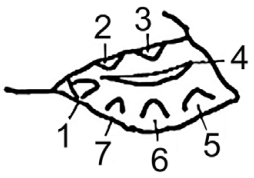

Figure 1. Apertural lamellae positions of *Laoma nerissa* (Hutton, 1883) (redrawn from Suter 1891: 284).

(Hutton, 1883), *L. ordishi* Climo n. sp., *L. labyrinthica* Powell, 1948 and *L. leimonias* (Gray, 1850) of shell and reproductive anatomy provides enough evidence for the reinstatement of *L. nerissa* as a valid species (apertural lamellae are described and discussed further in the taxonomic part and in the comparative remarks).

We consider that these five species are one set of species currently requiring inclusion in genus *Laoma s.str.,* as they form a natural group with comparable shell sizes, colour patterns, apertural barrier positions and anatomies (and possibly some *Phrixgnathus* species with *Laoma s.str.* characters). *Laoma s.str.* does not include species such as *L. ciliata*, *L. pirongiaensis*, *L. elegans* and *L. poecilosticta* listed in Suter (1913: 733), nor *L. mariae mariae* (Gray in Dieffenbach 1843), *L. mariae aupouria* Cumber, 1967 and *L. minuta* Climo, 1971 as listed in Spencer and Willan (1995: 41). These, and the ca. 130 mostly unnamed New Zealand species informally tag-named as '*Laoma*', are now seen as belonging to other natural groups to be listed in new genera or in subgenera of *Laoma s.lat.*, on a case-by-case basis. For example, six species, tagged in the Species 2000 list (Spencer, Marshall and Willan 2009) as '*Laoma*' spp., have already been formally described as members of *Kokopapa* Climo and Mahlfeld, 2011: *K. bispathulata*, *K. matarua*, *K. milleneri*, *K. mokihinui*, *K. rapahoe* and *K. unispathulata*, all Climo and Mahlfeld (2011).

METHODOLOGY

Animals were dissected with tools made of sections of 3 mm-square plastic strips with 0.11 mm diameter entomological pins melted into one end. Specimens were submerged in 70 percent ethanol. A Wild M7A stereomicroscope with drawing tube attached was used to draw the shells, and anatomical illustrations were drawn free hand. Shell dimensions were measured using a microscope eyepiece graticule. An Olympus SZX12 binocular microscope with an Olympus UC30 camera, and Zerene vers 1.04 (Littlefield) software were used to create high-resolution focus-stacked colour photos of the shells. Basemaps for the species distributions were created using the Fauna of New Zealand format. Fig. 1 illustrates Suter's nomenclature of apertural lamellae.

The species (re)descriptions follow a modern, commonly used nomenclature as laid out, for example, in Solem (1976, Fig. 36, p. 52–72 and 1983, pp. 15–23). For a key to reproductive anatomical characters please refer to Fig. 25 and related pages in Solem (1983). Both publications are available online.

Abbreviations

AM	Auckland Museum;
NMNZ	Museum of New Zealand Te Papa Tongarewa;
CM	Canterbury Museum.

Accession number identifications

AM	MA.
NMNZ	M.
CM	CM.

TAXONOMY

Superfamily PUNCTOIDEA Morse, 1864
Family PUNCTIDAE Morse, 1864
Subfamily LAOMINAE Suter, 1913

Genus *Laoma* Gray, 1850

Type species: *Bulimus*? (*L.*) *leimonias* Gray, 1850

Remarks: The systematics of the Laominae is poorly known as no intra- and intergeneric study with a comprehensive analysis of shell and reproductive morphology combined with molecular characters has been achieved yet. In this publication we provide comparative remarks on shell and reproductive characters of New Zealand laomine species sharing shell and/or anatomical characters that may eventually be corroborated by further molecular analysis as a subgroup within *Laoma s.str*. Thirty genera are currently recognised as belonging to the subfamily Laominae (WORMS Editorial Board 2019). The WORMS list reflects a compilation of available names from individual taxonomic publications but not much more. A more detailed analysis of other known and undescribed New Zealand endemic *Laoma* species is beyond the scope of the current paper, which predominantly deals with the reinstatement of *Endodonta nerissa* Hutton, 1884 as a distinct valid species, previously reduced to synonomy of *L. marina* by Suter (1891), and the introduction of a closely related new species, *L. ordishi* Climo n. sp. based on macro morphological characters. The necessary funds and institutional support are currently not available to us to embark on a full revision of Laominae, but we will attempt to publish all the accumulated knowledge gathered over a lifetime of research into Punctidae in a series of papers to make it accessible for further investigations.

Laoma ordishi Climo sp. nov.

(Figs 3C; 4D–E; 7E; 10; 14A)

Punctidae sp. 144 (NMNZ M.88107) Spencer *et al.* 2009: 218.

Material examined: Holotype (Fig. 10), MA73598, Taranga/Hen Island, SE of Whangarei, E1753468 N6018634, D.J. Roscoe, 16.10.2010. **Paratypes**, MA73599, same locality data as holotype; CM2019.89.1 – 2019.89.20, King Country, W of Te Kuiti, between Waikawau and Moeatoa, Whareorino Forest, E1749376 N5745385, Ian Payton, 12.11.2017, and NMNZ M.88107, Motairehe, Great Barrier Island, R.G. Ordish, 20.11.1964.

Other material: NMNZ: M.88107, M.28928, M.77515, M.57401, M.39140, M.39217, M.31011, M.56016, M.55807, M.76409, M.62609, M.70290, M.28934, M.88098, M.88100, M.88099, M.88108, M.72288, M.88033, M.88062, M.73303, M.85409, M.88084, M.24464, M.56748, M.48102, M.70169, M.88097, M.77583, M.69207, M.77640, M.70496, M.24614, M.75715, M.25516, M.99471, M.82615, M.97619, M.99332, M.97544, M.47830, M.78802, M.97305, M.82164, M.97765, M.51917, M.78665, M.46045, M.78894, M.88109, M.80249, M.82943, M.55176, M.36403, M.80358, M.99118, M.57641, M.77538,

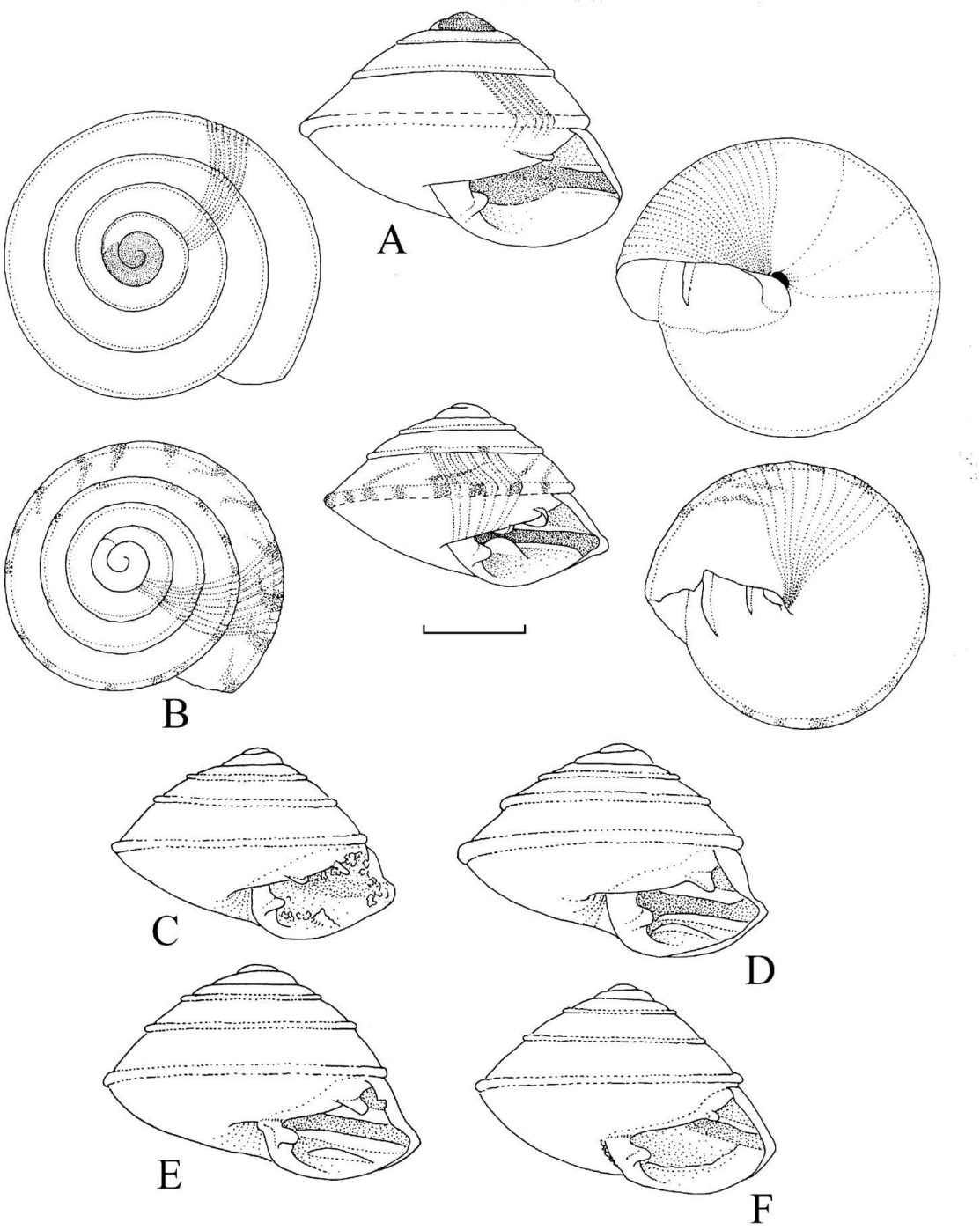

Figure 2. ***A***, *Laoma marina* (Hutton, 1883), lectotype, Remuera, Auckland, T.F. Cheeseman. ***B***, *Laoma nerissa* (Hutton, 1883), holotype, Remuera, Auckland, T.F. Cheeseman. ***C–F***, 'supposed syntypes' of *Laoma marina* (CM/M.1049; ***C*** and ***F***, *L. marina*; ***D*** and ***E***, *L. nerissa*), Auckland.

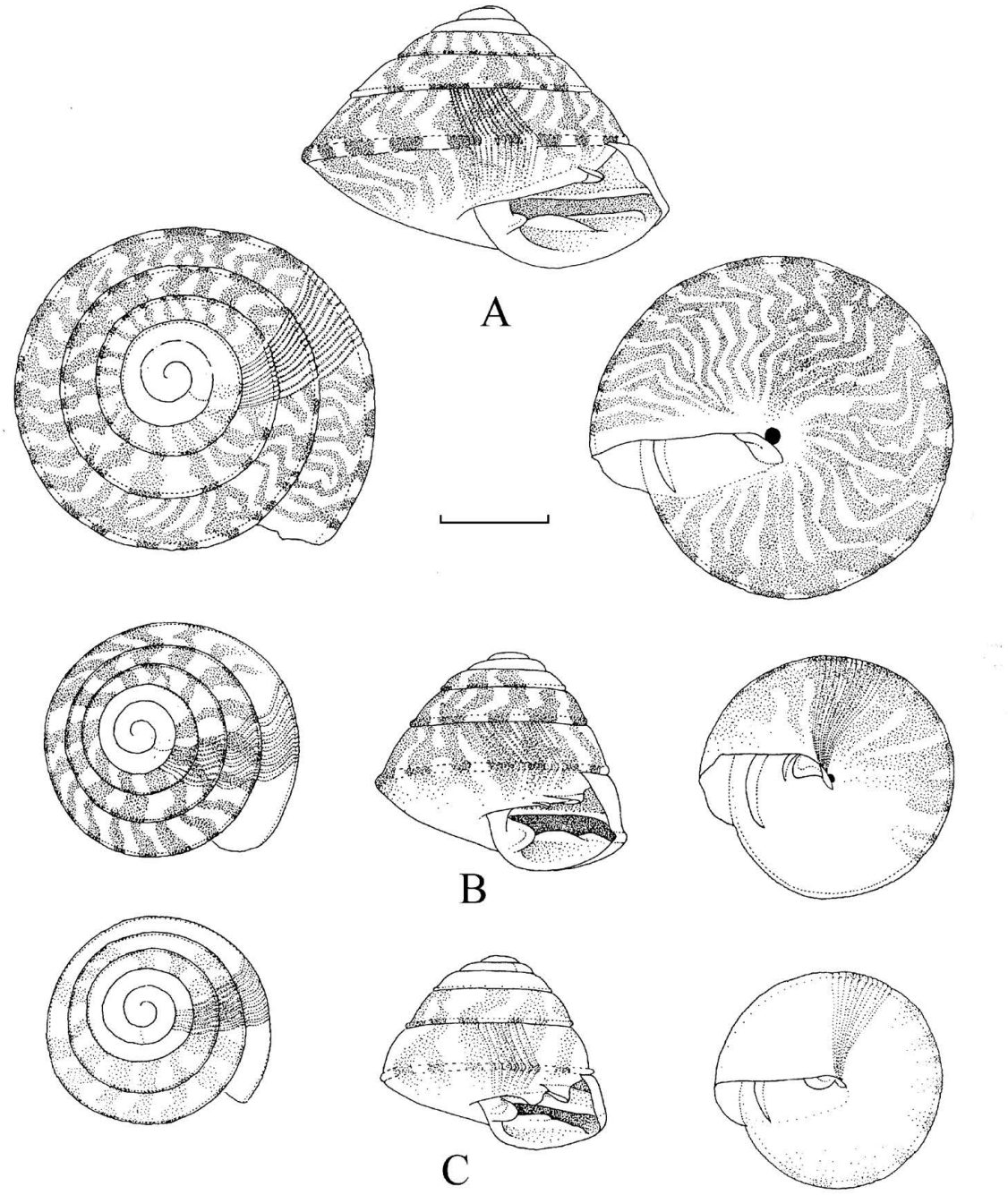

Figure 3. *Laoma*, group of *leimonias* (Gray, 1850). ***A***, *Laoma nerissa* (Hutton, 1883), Lost World Cave, Waitomo, Hamilton Junior Naturalists Club, 1970–72, NMNZ/M.54654. ***B***, *Laoma ordishi* n.sp., cave at Te Uku, Waikato, Hamilton Junior Naturalists Club, 1970–72, NMNZ/M.36403; ***C***, *Laoma ordishi* n.sp., voucher of Punctidae sp. 144, Motairehe, Great Barrier Island, R.G. Ordish, 20.11.1964, NMNZ/M.88107.

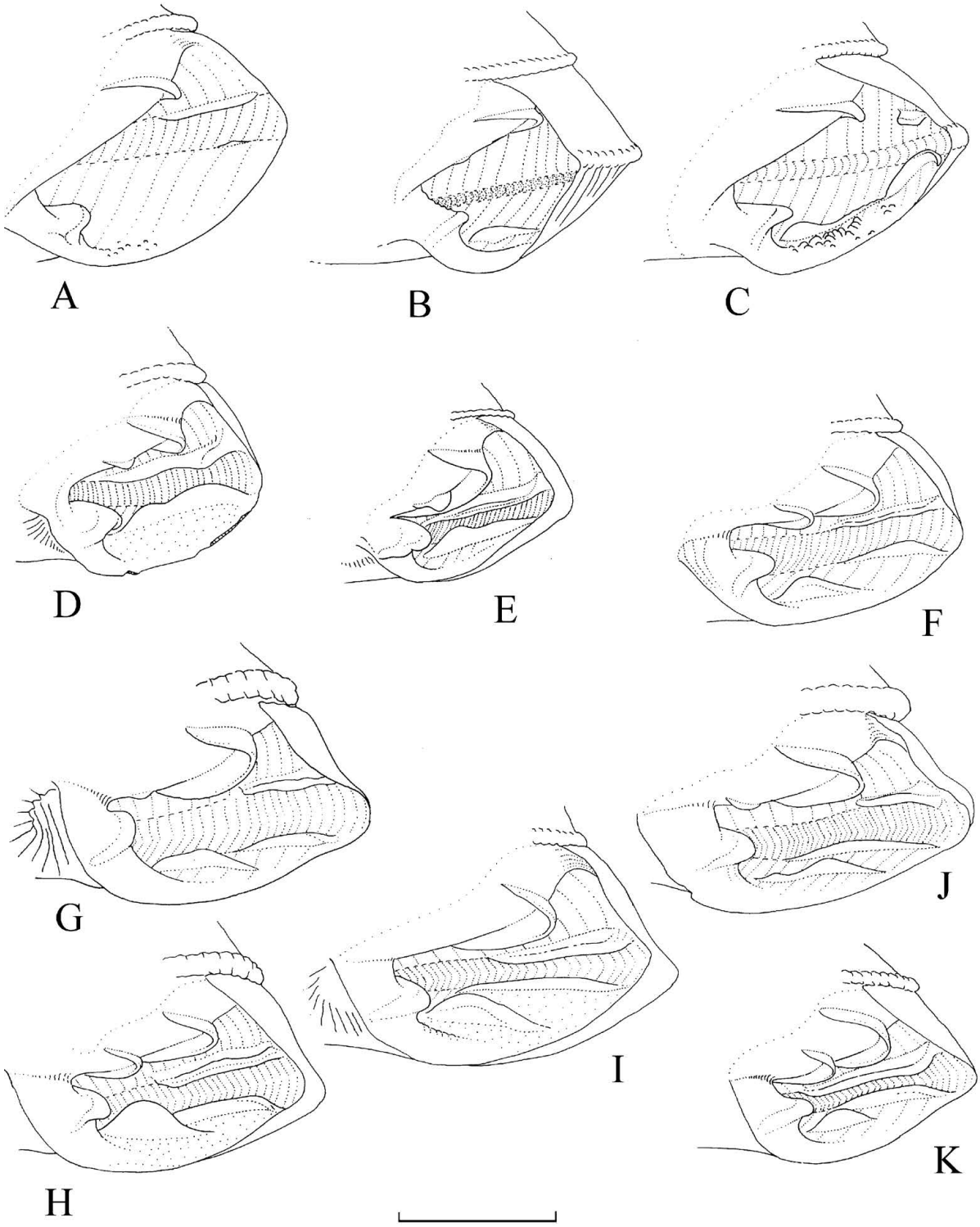

Figure 4. *Laoma*, group of *leimonias* (Gray, 1850), apertural teeth and plaits: ***A–C***, *Laoma marina* (Hutton, 1883). ***D–E***, *Laoma ordishi* n.sp.. ***F–K***, *Laoma nerissa* (Hutton, 1883). ***A***, broadleaf and mamaku litter, Jones Bush, Waiuku, F.M. Climo & D.J. Roscoe, 11–12.2.1981, NMNZ/M.78540. ***B–C***, Woodlands, Waitakere Ranges, Auckland. J.F. Goulstone, 20.9.1967, NMNZ/M.38388. ***D***, cave at Te Uku, Hamilton Junior Naturalists Club, 1970–72, NMNZ/M.36403. ***E***, paratype (Te Papa), Motairehe, Great Barrier Island, R.G. Ordish, 20.11.1964, NMNZ/M.28928. ***F***, Hen Island, C.A. Fleming, 26.2.1934, NMNZ/M.88109. ***G***, Mangatawhiri, Auckland, B.F. Hazelwood, 9.10.1976, NMNZ/M.55432. ***H***, Kaimai Range, A.C. O'Connor, -.4.1941, NMNZ/M.88096. ***I***, Lost World Cave, Waitomo. Hamilton Junior Naturalists Club, 1970–72, NMNZ/M.54659. ***J***, Hunua Gorge, Auckland, J.F. Goulstone, 3.10.1967, NMNZ/M.38381. ***K***, cave, Te Uku. Hamilton Junior Naturalists Club, 1970–72, NMNZ/M.39291. Scale line 1 mm.

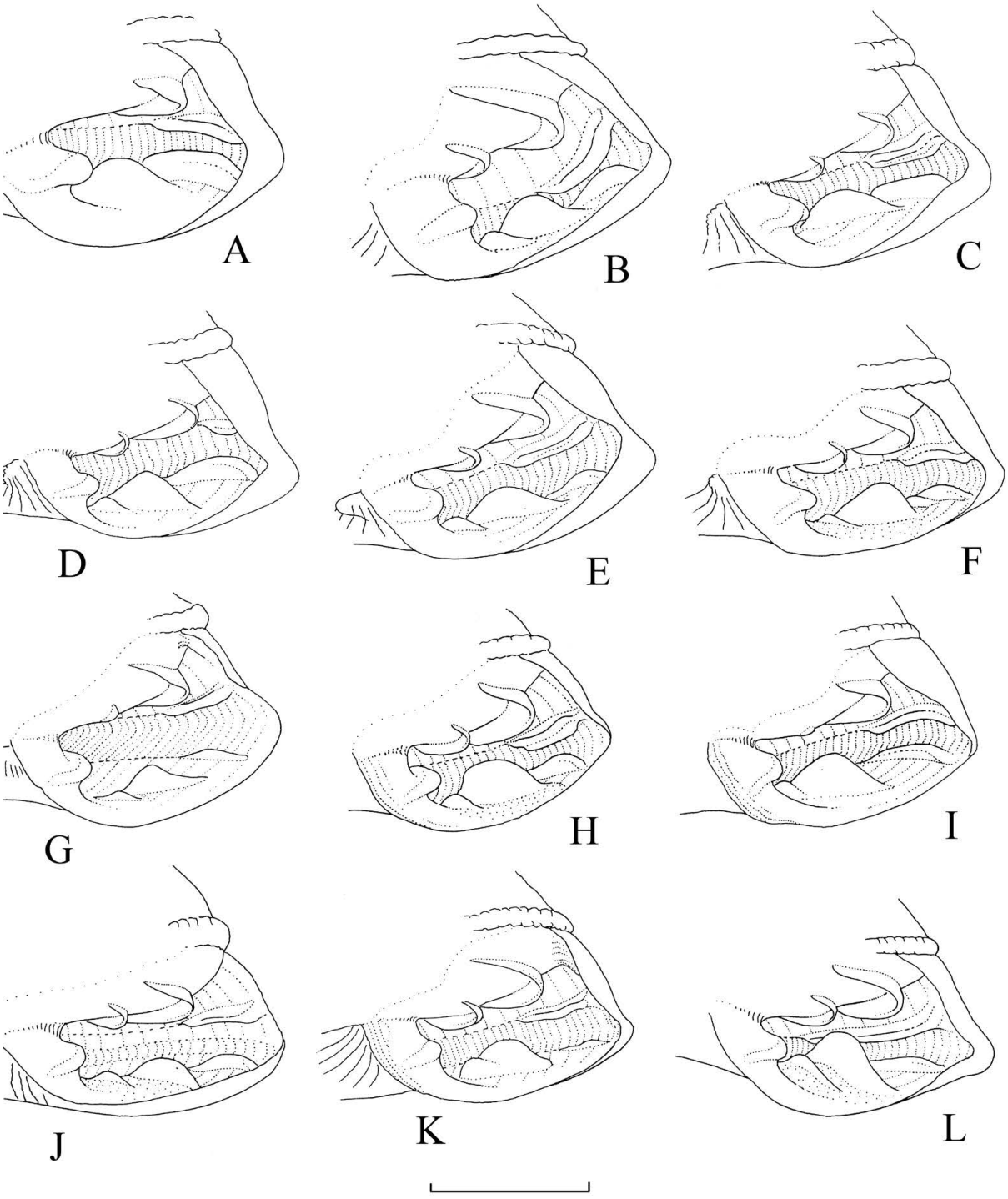

Figure 5. *Laoma*, group of *leimonias* (Gray, 1850), *Laoma nerissa* (Hutton, 1883), apertural teeth and plaits from 11 localities (from north to south): ***A–B***, Mokau River mouth, F.M. Climo, 5.3.1977, NMNZ/M.56728. ***C***, Clifton–Taumarunui boundary, inland Taranaki, F.M. Climo, 8.3.1977, NMNZ/M.56697. ***D***, Dawson Falls, Mt Taranaki, 3100', M.P. Buchler, NMNZ/M.14039. ***E***, Tangoio, Hawke Bay, N43/307610, D.J. Roscoe, 25.2.1968, NMNZ/M.46424. ***F***, Taoroa, Taihape, A.C. O'Connor, -.6.1942, NMNZ/M.88095. ***G***, Rock Rd, Konini, Wairarapa, B.F. Hazelwood, 1976, NMNZ/M.56257. ***H***, northeastern Kapiti Island, W.F. Ponder, -.4.1956, NMNZ/M.24898. ***I***, D'Urville Island, R.A. Cumber, 8.4.1941, NMNZ/M88106. ***J***, Lichfields Bay, Manaroa, Marlborough, W.F. Ponder, 7.1.1959, NMNZ/M.24945. ***K***, Pelorus Bridge, Nelson, A.C. O'Connor, -.1.1949, NMNZ/M.88105. ***L***, Richmond Reservoir, Nelson, F.M. Climo. 25.11.1967, NMNZ/M.38405. Scale line 1 mm.

M.80191, M.88789, M.70863, M.63375, M.76750, M.38477, M.8830, M.97311, M.104400, M.96607, M.99409, M.100263, M.104520, M.114620.

Description: Shell (Figs 3C; 4D–E; 10). Small, approx. 2.45 mm wide and 2.1 mm high at 5.5 whorls, trochiform, carinated, imperforate, thin, transparent, whitish to pale buff streaked with brown to dark brown zigzag bands. Suture impressed, strongly margined. Spire conic, slightly higher than height of aperture; outlines weakly convex. Protoconch of 1.5–1.75 whorls, sculptured with ~16 spiral lirae and weak irregular oblique axial ridges. Teleoconch whorls weakly convex, periphery carinate and ornamented with equidistant brown bands; base convex. Sculpture consisting of weakly oblique prominent and narrowly-spaced axials, these slightly weaker on base. Aperture oblique, rhombic, with one strongly calcareous columellar lamella, one upper parietal crescent-shaped thinner and one mid-parietal shorter and thicker lamella. Palatal wall with one short, thick lamella about midway. Basal part inside aperture with a calcareous thickening from columella to carina and two protuberances. Peristome sharp; columella short and arcuate; inner lip reflexed, thickened and sometimes with a calcareous smear across the umbilical depression.

Reproductive system (Fig. 7E; only dissected male genitalia available). Phallus duct long and cylindrical, tapering slightly towards atrium; retractor muscle attached apically. Vas deferens enters phallic lumen through a simple pore just below retractor muscle. Interior of phallus ornamented with three apical traverse pilasters, a median oval pilaster flanked by two wing-shaped thin folds with short apical bifurcations. The median part of the lumen wall is folded into three latitudinal ridges (perhaps indicative of a reduced sphincter?), and below these ridges the interior wall is partially but smoothly and uniformly thickened. A third, longitudinal, highly folded, ruffled, irregular pilaster fills most of the abapical part of the lumen.

Etymology: Named in memory of former colleague and entomologist at Museum of New Zealand Te Papa Tongarewa, R. G. Ordish, who collected some of the early material of *Laoma ordishi* n. sp.

Laoma marina (Hutton, 1883)

(Figs 2A,C,F; 4A–C; 7A–B; 11; 14B)

Punctidae sp. 145 (NMNZ M.88110) Spencer *et al*. 2009: 218.

Material examined: Lectotype, CM/M.1402.1, Remuera, Auckland. **Paralectotype**, CM/M.1401.2, same data.

Other material: NMNZ: M.88110, M.38398, M.81769, M.63321, M.63454, M.75578, M.88111, M.63438, M.58164, M.76291, M.88112, M.97512, M.80357, M.73569, M.48427, M.82899, M.32180, M.48548, M.47784, M.80304, M.61815, M.38404, M.75862, M.68654, M.77791, M.55832, M.57864, M.75323, M.24940, M.63274, M.63251, M.78540, M.38410, M.63307, M.89932, M.99314, M.88505, M.99525, M.116721, M.72363, M.84771, M.84772, M.84789, M.102706, M.84667, M.104021, M.114445, M.113678, M.97617, M.113648, M.99257, M.63412, M.113688.

Redescription: Shell (Figs 2A,C,F; 4A–C; 11). Small, 2 mm wide and 1.38 mm high at 4.25 whorls, trochiform, carinated, very narrowly umbilicated, thin, transparent whitish to pale buff streaked with reddish brown to brown zigzag lines. Suture impressed, margined. Spire conic, height equal to height of aperture; outlines slightly convex. Protoconch of 1.5 whorls, sculptured with 15+ narrowly-spaced fine spiral lirae. Teleoconch whorls flat, periphery carinate and ornamented with equidistant brown bands; base convex. Sculpture consisting of fine oblique growth wrinkles; last whorl somewhat concave below the peripheral keel. Aperture somewhat oblique, rhombic, with one strong columellar lamella, one upper long, thin parietal lamella, one long, thin palatal lamella just above the carinate periphery, and a basal callosity, which is sometimes developed into a diagonal irregular hump or is absent in some specimens. Peristome sharp; columella short, arcuate; inner lip reflexed and partially covering narrow, deep umbilicus.

Reproductive anatomy (Fig. 7A, B). Gonads relatively large, bilobed; each lobe consisting of seven to eight elongate acini. Albumen gland squarish-round, alveoli small; round talon on stalk buried in albumen gland. Prostatic gland bunched with large folds; uterus of similar size, surface smooth. Oviduct twice as large as spermathecal base, both round and slender. Apical part of spermatheca ovate. Hermaphroditic duct short, broad and kinked. Vagina relatively short, cylindrical. Vas deferens enters phallus through a simple pore adjacent to the retractor muscle near apex of phallus. Phallus with a constriction just above midway of lumen, which tapers off rapidly towards atrium. Apical half of phallus lumen interior adorned by three longish pilasters, joined in a broad base to lumen wall. Interior lumen wall below the apical pilasters and constriction uniformly smooth. Atrium relatively short.

Remarks: Punctidae sp. 145 (known by the tag name '*Laoma paucilamellata*') was used in the past for a conchological variant of *L. marina*. The voucher of Punctidae sp. 145 was collected by J.F. Goulstone from Woodlands Park, Auckland in 1967. Other specimen lots in the Te Papa Tongarewa collection that may have been associated either with this voucher or *Laoma marina* sensu Hutton lots will include extremely low spired specimens with weakly developed apertural lamellae and shell sculpture, which cannot be separated easily from the range of shell variation shown by *L. marina*. At present DNA material is insufficiently sampled to advance taxonomy further in this case (pers. comm. F.J. Brook).

Laoma nerissa (Hutton, 1883) reinstated

(Figs 2B,D–E; 3A; 4F–K; 5A–K; 7C–D; 12; 13)

Endodonta nerissa Hutton, 1883: 476; Hutton, 1884a: 176; Hutton, 1884b: 196.

Laoma marina Suter 1891: 285 (in part and also for authors from here on except Bogich *et al*. 2012); Pilsbry (1892: 57–58); Hedley and Suter (1893: 646); Suter (1893: 274); Suter (1913: 735–736); Powell (1979: 325, plate 59) (= *L. nerissa*); Marshall (1995: 498); Freeman *et al*. (1997: 32); Spencer *et al*. (2009: 217); Spencer *et al.* (2016).

Material examined: Holotype, CM/M.1400, Remuera, Auckland.

Other material: NMNZ: M.56687, M.55960, M.38696, M.68698, M.29654, M.46388, M.55432, M.32061, M.56672, M.56732, M.31957, M.31984, M.45801, M.45922, M.68572, M.32063, M.96916, M.98089, M.88092, M.45865, M.48439, M.56947, M.38988, M.96950, M.68073, M.24893, M.63334, M.39061, M.98470, M.96864, M.57649, M.24894, M.98374, M.98623, M.98467, M.92603, M.93097, M.98644, M.98066, M.97789, M.89318, M.98174, M.88667, M.98486, M.98920, M.96859, M.87678, M.87508, M.92877, M.89374, M.92635, M.97722, M.98562, M.96899, M.98533, M.98192, M.97794, M.97771, M.99576, M.96878, M.98499, M.97013, M.97827, M.97793, M.77345, M.73302, M.72250, M.72195, M.70280, M.722287, M.56204, M.14156, M.78925, M.78769, M.79053, M.72330, M.70571, M.76200, M.70472, M.72269, M.78919, M.72392, M.75642, M.80280, M.69029, M.76226, M.75945, M.79684, M.75818, M.75778, M.76411, M.76279, M.75928, M.80823, M.76168, M.56737, M.75852, M.29105, M.24897, M.22204, M.79982, M.80091, M.38401, M.80073, M.88101, M.46857, M.24891, M.24899, M.88103, M.24895, M.88102, M.24902, M.88105, M.24889, M.55526, M.79963, M.24901, M.24888, M.69391, M.70766, M.37031, M.37036, M.88104, M.108030, M.107447, M.107374, M.116183, M.108108, M.108164, M.88606, M.98678, M.98181, M.88521, M.89552, M.99594, M.89464, M.89456, M.89534, M.89391, M.99312, M.88754, M.89490, M.88562, M.89387, M.99555, M.114878, M.114918, M.113704, M.89431, M.114948, M.89785, M.98130, M.113787, M.98699, M.93113, M.98569, M.92655, M.97117, M.92612, M.98606, M.92734, M.98435, M.99874, M.101553, M.102759, M.102836, M.103593, M.103148, M.102001, M.104506, M.103498, M.103477, M.102790, M.102745, M.116630, M.114478, M.116582, M.115000, M.69252, M.101841, M.69469, M.106713, M.103676, M.101383, M.101494, M.115011, M.116487, M.101925, M.116045, M.115725, M.114492, M.51789, M.113661, M.102819, M.104298, M.101458, M.114662, M.116033, M.115862, M.116216, M.115896, M.116016, M.116072, M.107818, M.116124, M.103930, M.101514, M.101870, M.101988, M.104093, M.104200, M.102809, M.101373, M.101090, M.104377, M.101703, M.116084, M.103984, M.104825, M.101767, M.104056, M.101329, M.104683, M.106751, M.105338, M.106396, M.104914, M.105197, M.101954, M.105075, M.105321, M.105232, M.103083, M.101945, M.105410, M.106041, M.105868, M.106355, M.105294, M.69561, M.57121, M.69614, M.38405, M.24896, M.69639, M.22571, M.32066, M.25468, M.80146, M.24945, M.23597, M.88106, M.105101, M.69684, M.56975, M.81917, M.69671, M.105256, M.105175, M.108211, M.109737, M.108471, M.108648, M.100737, M.100789, M.107336, M.108566, M.108385, M.108619, M.107232, M.107273, M.62969, M.108432, M.69295, M.48513, M.46465, M.88085, M.47246, M.55939, M.46555, M.38379, M.38397, M.55952, M.52364, M.88089, M.25412, M.38386, M.46492, M.14272, M.88086, M.69119, M.32065, M.37508, M.24892, M.88091, M.63320, M.38381, M.88090, M.51834, M.22323, M.88088, M.88087, M.68586, M.56600, M.25323, M.45940, M.38387, M.14521, M.51756, M.45654, M.82032, M.24952, M.47911, M.56209, M.36404, M.39177, M.39291(mixed lot), M.57212, M.57172, M.57060, M.68602, M.62578, M.68583, M.68991, M.57299, M.57004, M.56776, M.24900, M.31081, M.38384, M.56222, M.38383, M.68439, M.55920, M.62637, M.85352, M.85308, M.78830, M.85417, M.85949, M.86112, M.82310, M.81681, M.77790, M.81847, M.81872, M.85529, M.82399, M.82024, M.78464, M.81815, M.82891, M.85720, M.78498, M.78730, M.85758, M.82206, M.77638, M.79853, M.80379, M.80193, M.80136, M.79779, M.82484, M.81957, M.82576, M.82239, M.82110, M.72900, M.52242, M.52050, M.85460, M.22068, M.75693, M.72760, M.75684, M.46433, M.70495, M.73287, M.46552, M.70661, M.46548, M.70866, M.72455, M.70457, M.29028, M.72872, M.72272, M.73349, M.70718, M.72424, M.78743, M.46464, M.72134, M.56257, M.52184, M.52038, M.46452, M.56131, M.1420, M.77249, M.77249, M.55733, M.46513, M.46551, M.31133, M.46461, M.56512, M.46509, M.48467, M.46430, M.46553, M.46545, M.56261, M.47862, M.76193, M.76122, M.48581, M.46431, M.76871, M.80163, M.76909, M.55298, M.46565, M.98446, M.46503, M.62724, M.46472, M.47161, M.75655, M.76924, M.68982, M.68045, M.39113, M.61719, M.45767, M.51939, M.47201, M.88094, M.46396, M.47970, M.47934, M.22369, M.37652, M.88095, M.55250, M.14148, M.31087, M.46375, M.68803, M.46390, M.46380, M.56697, M.46497, M.14499, M.69135, M.14236, M.36819, M.24898, M.46491, M.46410, M.46383, M.29978, M.46389, M.61860, M.46402, M.46561, M.46485, M.45711, M.56995, M.46448, M.46500, M.88096, M.69973, M.56985, M.47723, M.61991, M.57007, M.46562, M.68618, M.31208, M.63141, M.47683, M.55240, M.45894, M.69550, M.69504, M.70030, M.57759, M.63502, M.47797, M.57681, M.57087, M.48033, M.25093, M.55322, M.68842, M.68872, M.46406, M.63534, M.63379, M.56659, M.25232, M.56728, M.30056, M.61498, M.45691, M.14039, M.14452, M.57438, M.58254, M.68921, M.67907, M.46458, M.68541, M.24942, M.46424, M.46514, M.57865, M.56559, M.68891, M.57191, M.57872, M.97705, M.46550, M.32002, M.61974, M.52345, M.56628, M.56377, M.58282, M.57776, M.46447, M.32064.

Redescription: Shell (Figs 2B,D–E; 3A; 4F–K; 5A–K; 12; 13). Small, 2.32 mm wide and 1.41 mm high at five whorls, trochiform, carinated, narrowly umbilicated, thin transparent, whitish to pale buff streaked with brown to dark brown rather narrow zigzag lines. Suture impressed, margined. Spire conic, higher than height of aperture; outlines flat to slightly convex. Protoconch of 1.5–1.75 whorls, pustulate, with 10–12 spiral lirae broken up by irregular oblique axial ridges resulting in a beaded sculpture. Teleoconch whorls flat to slightly convex, periphery carinate and ornamented with equidistant brown bands; base convex. Sculpture consisting of

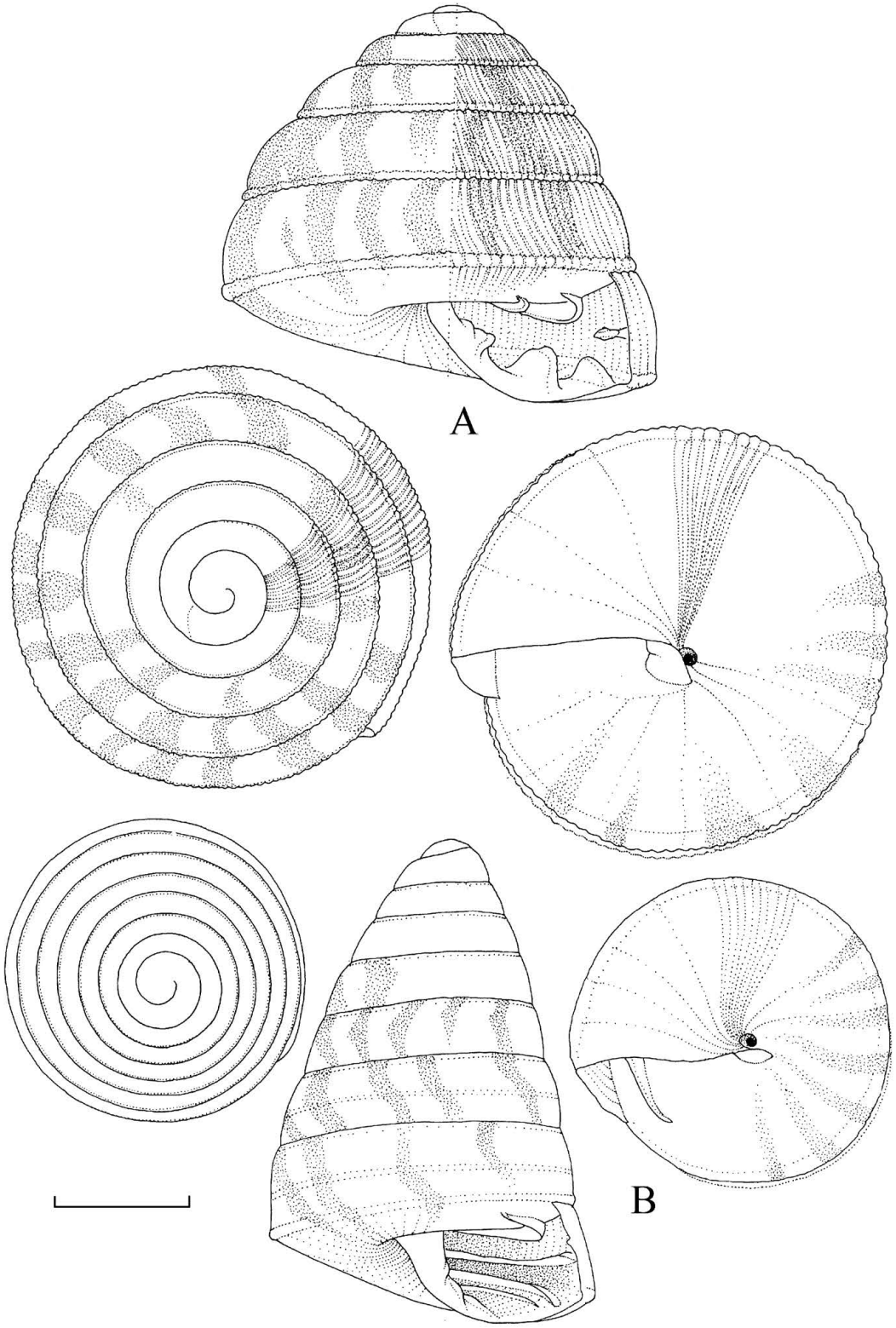

Figure 6. *Laoma*, group of *leimonias* (Gray, 1850). ***A***, *Laoma labyrinthica* Powell, 1948, *Brachyglottis*, 100' below camp, Castaway Valley, Great King Island, F.M. Climo, 28.11.1970, NMNZ/M.47288. ***B***, *Laoma leimonias*, broadleaf and mamaku litter, Jones Bush, Waitutu, Auckland, F.M. Climo and D.J. Roscoe, 11–12.2.1981, NMNZ/M.78562. Scale line 1 mm.

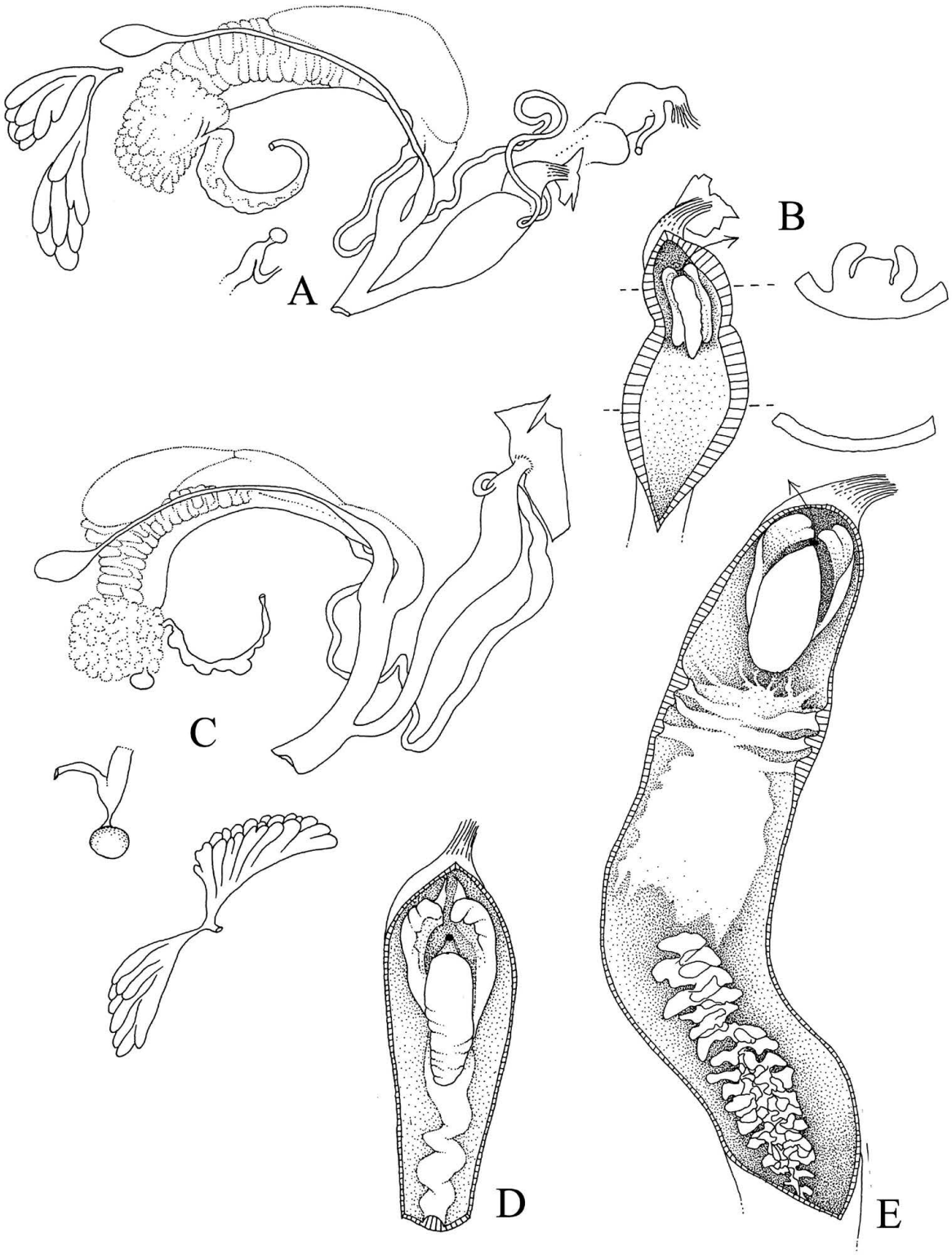

Figure 7. *A–B*, *Laoma marina* (Hutton, 1883), whole reproductive system and dissected epiphallus, Woodlands, Waitakere, Auckland, N. Douglas, 13.8.1967. *C–D*, *Laoma nerissa*, (Hutton, 1883), whole reproductive system and dissected epiphallus, Naenae, Hutt Valley, Wellington, F.M. Climo, 24.2.1966. *E*, *Laoma ordishi* n.sp., dissected epiphallus, 4 miles S of Wellsford, southern Northland, F.M. Climo, -.3.1968.

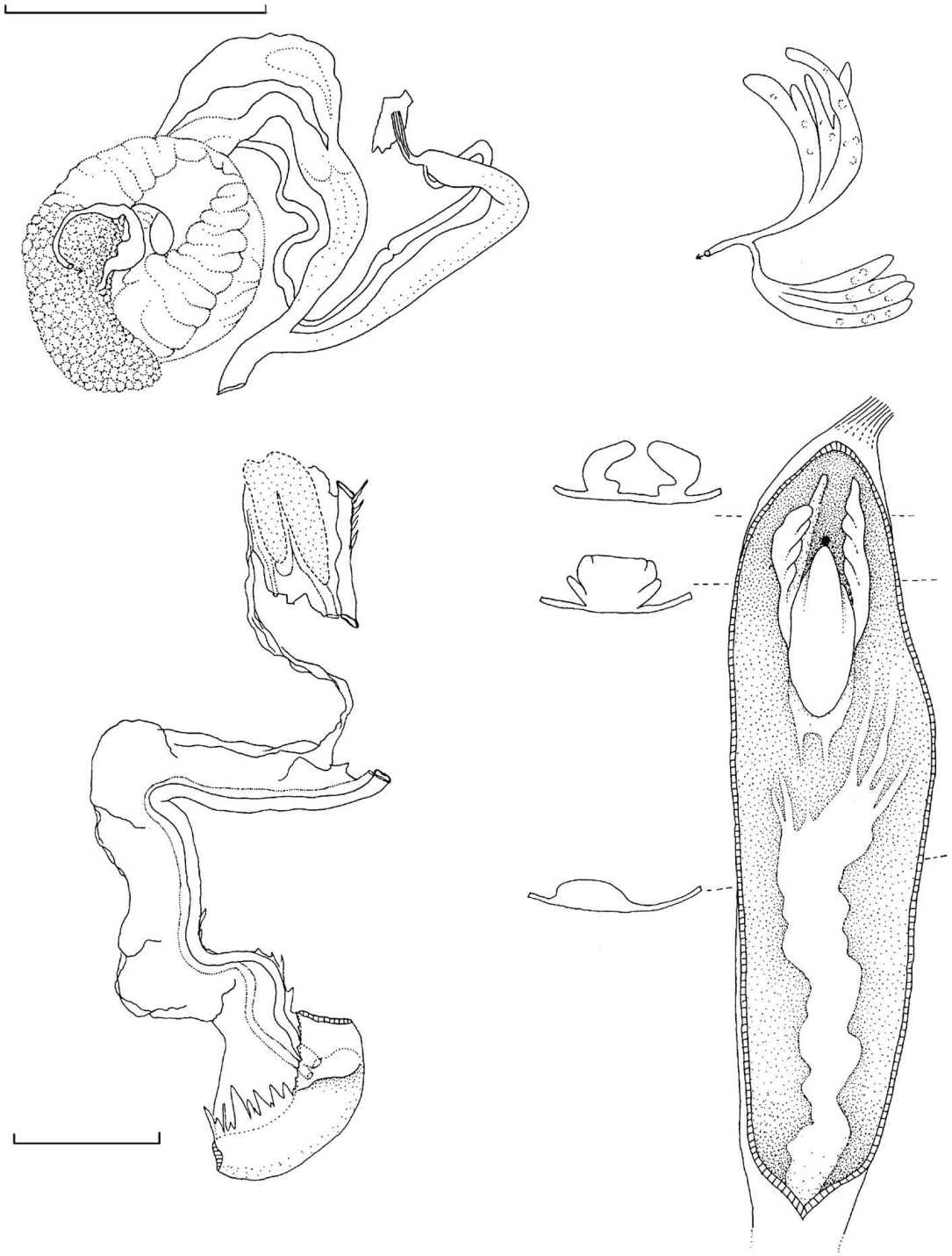

Figure 8. *Laoma*, group of *leimonias* (Gray, 1850). *Laoma leimonias*, pallial roof, whole reproductive system and dissected epiphallus, Mangatawhiri, Hunua, Auckland, N. Douglas, 3.10.1967. Scale line 1 mm.

Figure 9. *Laoma labyrinthica* Powell, 1948. Three Kings Islands, Great King, below camp, L01/320828, 100 m asl, F.M. Climo, 14.11.1970. Scale line 1 mm.

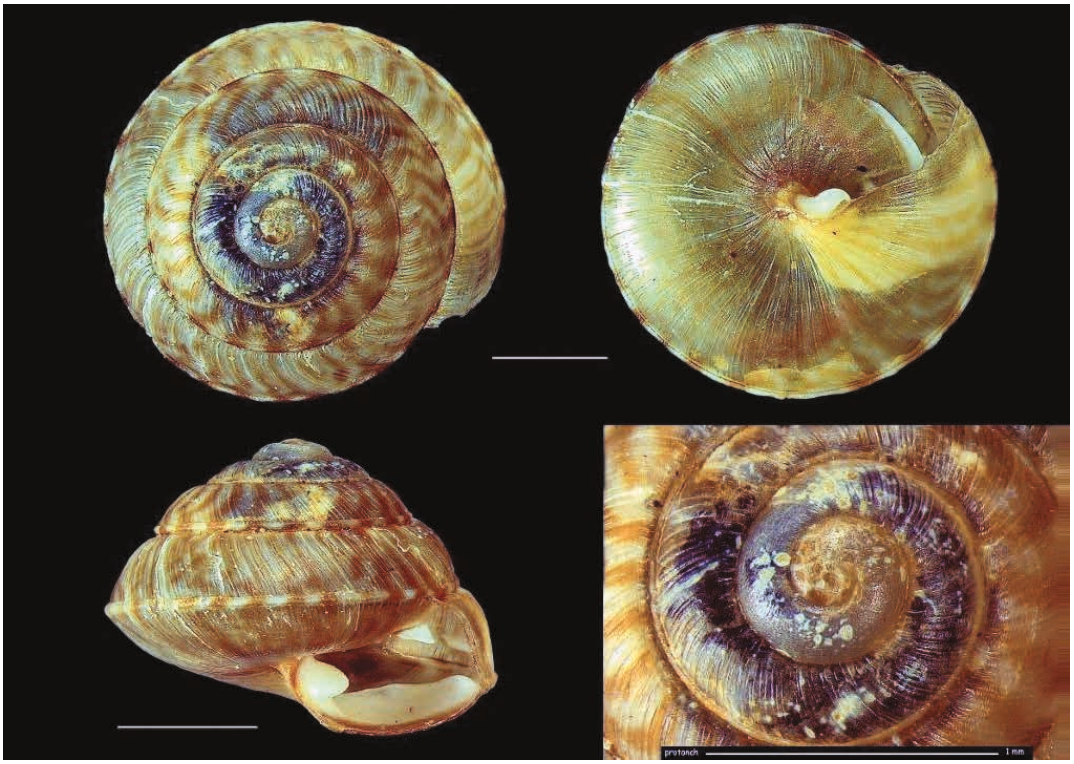

Figure 10. *Laoma ordishi* Climo n. sp., holotype, MA73598, Taranga/Hen Island, SE of Whangarei, E1753468 N6018634, D.J. Roscoe, 16.10.2010. Scale line 1 mm.

Figure 11. *Laoma marina* (Hutton, 1883), Mount Pirongia, King Country, E1786653 N5795052, K. Mahlfeld, 3.5.2018. Mainly tawa, 468 m asl. Scale line 1mm. (Note: calcareous thickening weak in this specimen).

Figure 12. *Laoma nerissa* (Hutton, 1883). Namunamu, Himatangi, Turakina Valley, E1809613 N 5581912, I.A.N. Stringer, 15 September 2007. Scale line 1 mm.

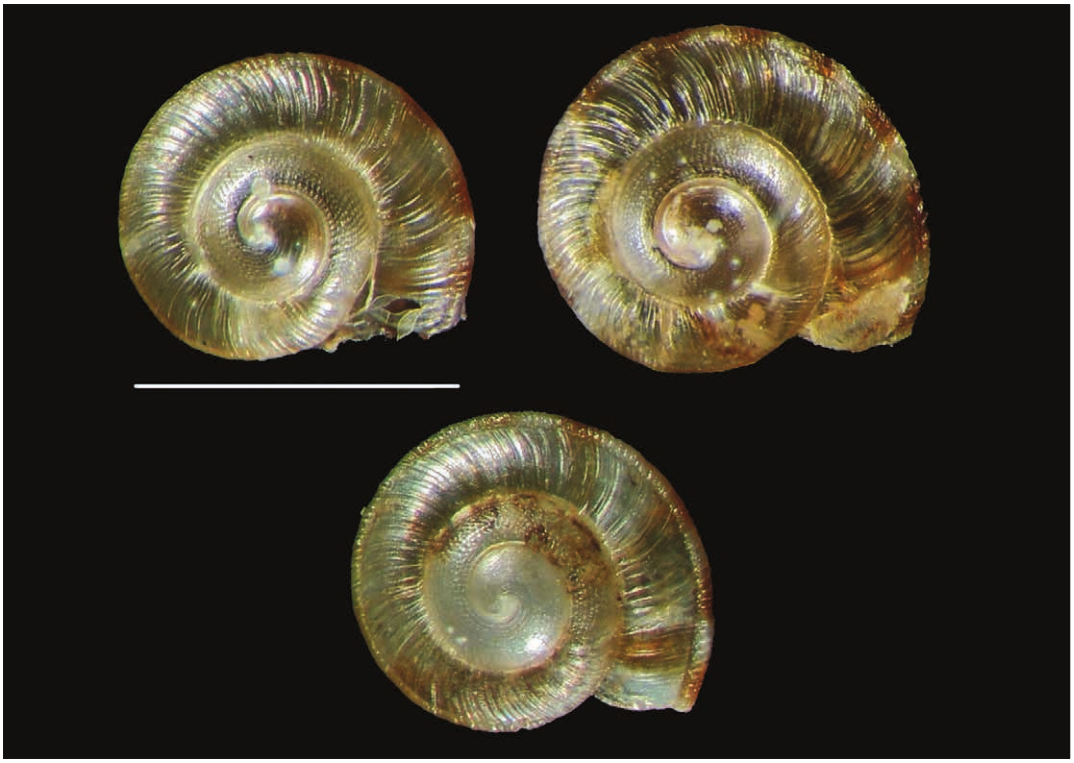

Figure 13. Close-up of protoconch sculpture of *Laoma nerissa* (Hutton, 1883). Mangakahia Stream W of Te Kuiti and NW of Taupo, E1758764 N5758472, L. Daglish, 10.8.2007. Beneath limestone bluffs. Scale line 1 mm.

prominent oblique growth wrinkles; last whorl sometimes slightly concave below the peripheral keel. Aperture oblique, rhombic, with one strong columellar lamella, one upper crescent-shaped thin parietal lamella, one smaller mid-parietal crescent-shaped lamella, the latter often nearly fully reabsorbed to leave just a little bump. Inner outer lip with one long thin palatal lamella just above the carinate periphery and three basal cone-shaped lamellae, which are fused in some specimens. Peristome sharp; columella short arcuate; inner lip reflexed and partially covering narrow, deep umbilicus.

Reproductive system (Fig. 7C–D). Gonads relatively large, bilobed; each lobe consisting of many elongate acini. Albumen gland squarish-round, alveoli small; round talon on stalk buried in albumen gland. Prostatic gland bunched with large folds; uterus of similar size, surface smooth. Oviduct and spermathecal base of similar proportions, both round, slender and tapering towards uterus and prostate respectively. Apical part of spermatheca ovate. Hermaphroditic duct short, broad and kinked. Vagina relatively long, cylindrical. Vas deferens enters phallus through a simple pore just below the retractor muscle near apex of phallus. Phallus tapers slowly towards atrium. Apical half of interior adorned by a large, longish oval pilaster flanked by crescent-shaped folded pilasters. Below the three apical pilasters, interior ornamented with a long, wavy, longitudinal pilaster or uniformly smooth walls; a trace of a constriction is discernible about midway of phallic lumen.

Remarks: Suter based his comparisons of *L. marina* and *L. nerissa* on a large sample from Auckland, one of the areas where the species' ranges overlap. Charles Mousson provided the sample, which he collected on the lava fields of Mount Wellington, Auckland. Hutton's samples were collected from Remuera, Auckland by T.F. Cheeseman (according to Dr A.W.B. Powell's notes lodged in Auckland Museum).

DISCUSSION

Comparative remarks

L. marina has a larger shell with fewer apertural lamellae, and weaker shell sculpture and carina than *L. nerissa* and *L. ordishi* n. sp., as shown by shell drawings of the type material and colour photos. Shell shape is also more depressed in *L. marina* (Figs 2 and 11) than in the slightly taller-spired *L. nerissa* (Figs 2 and 12) and *L. ordishi* n. sp. (Figs 3 and 10), which also tends to be more beehive-shaped. All three species have one prominent columellar lamella but differ in other barriers (Figs 4 and 5). *L. ordishi* n. sp. shares with *L. marina* a broad calcareous band from columella to carina. Generally, *L. nerissa* has two long parietal lamellae, one larger upper one and a smaller lower one; a long palatal lamella parallel to and just above the periphery and three large basal lamellae. Some minor variation (as illustrated in Figs 4 and 5), occurs depending on the growth stage and whether all lamellae are fully developed, or more

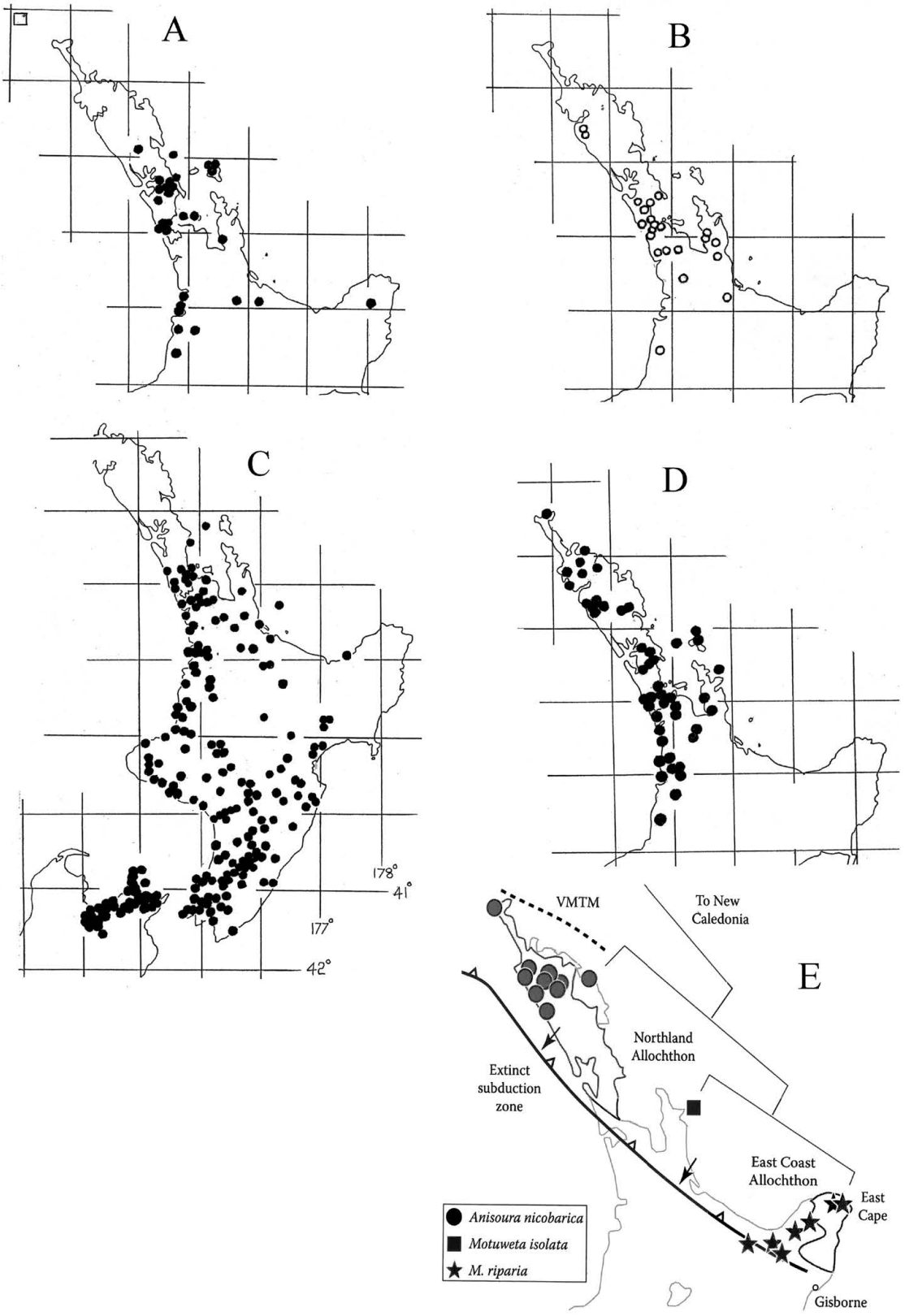

Figure 14. Distributions of *Laoma leimonias* group species. ***A***, *Laoma labyrinthica* Powell, 1948 (open square); *Laoma ordishi* n. sp. (filled circle). ***B***, *Laoma marina* (Hutton, 1883) (open circle). ***C***, *Laoma nerissa* (Hutton, 1883) (filled circle). ***D***, *Laoma leimonias* (Gray, 1850) (filled circle); ***E***, distribution and phylogeny of New Zealand tusked weta, *Motuweta* and *Anisoura* and associated allochthonous terranes; VMTM=Vening Meinesz transform margin; arrows indicate the former southeast rollback of subduction zone, now extinct (redrawn from Heads 2017: Fig. 5.6, p. 154).

rudimentary. Protoconch and teleoconch sculpture and carina are stronger in *L. nerissa* coupled with a slightly more open umbilicus, which is very small to obsolete in *L. marina* and *L. ordishi* n. sp. Teleoconch axial sculpture is weakest in *L. marina* but stronger and of similar grade in *L. ordishi* n. sp. and *L. nerissa*. The shells of *L. ordishi* n. sp. are the smallest of the three species. All three species also differ in protoconch sculpture (Figs 10–13). In contrast, *Laoma leimonias* (Gray, 1850) is glossy and a much taller-spired species with more shell whorls, while sharing a certain type of reproductive morphology with *L. nerissa*, *L. marina* and *L. ordishi* n. sp. (Figs 6 and 8). *L. labyrinthica* Powell, 1948 has the most heavily sculptured shell and barrier configuration (Figs 6 and 9) with a colour pattern of broad axial brown bands, but reproductive anatomy is unknown.

Dissections of the male reproductive systems of *L. marina* (Fig. 7A,B) and *L. nerissa* (Fig. 7C,D) show a weaker development of pilasters in the upper lumen and a more conspicuous constriction in the upper third of the lumen in *L. marina* compared to *L. nerissa*. The junction between epiphallus/phallus in *L. ordishi* n. sp. (Fig. 7E) is not marked by a constriction as in *L. marina* and is, as already mentioned, weaker in *L. nerissa*. The lumen wall is thinner in *L. ordishi* n. sp. and the median upper pilaster is larger while the pilasters on each side are thinner. The area of constriction is still marked by three latitudinal thin ridges followed by a thickened patch mid-lumen and a series of irregular, smaller pilasters on the lower lumen wall. The terminal male lumen interior is similar in *L. leimonias* without a constriction in the male terminal duct (Fig. 8).

All species addressed here share shell and anatomical characters which suggest that they form a group of related lamellate species within *Laoma s.str.* The non-lamellate species *Phrixgnathus murdochi* Suter, 1894, *P. sciadium* (Pfeiffer, 1857) and another unnamed closely related species may also warrant inclusion into *Laoma s.str.* based on shell and reproductive features. This hypothesis could be tested with molecular data in future.

Conservation status and geographic distributions

In New Zealand, the Department of Conservation (DOC) maintains and publishes lists of the conservation status of native species based on population size, area of occupancy, population trends, and type and severity of threats. The highest threat category is nationally critical, while the lowest rank is naturally uncommon (Townsend *et al*. 2008). Currently, over 600 terrestrial snails and slugs are of some conservation concern (Mahlfeld *et al*. 2012; an update will be published this year). *Laoma marina* is sparsely distributed from Auckland and Coromandel northwards to Hokianga Harbour with an outlier in the King Country and probably not threatened, but sparser than the other mainland species. *L. nerissa* is found from Auckland southwards with its range extending to Marlborough Sounds and Nelson in the South Island (Fig. 14). This species is common and not threatened. *L. labyrinthica* is endemic to Great King, Three Kings Islands and as an island endemic is automatically classified as naturally uncommon. *L. ordishi* n. sp. occurs from Taranga Island south to South Waikato and East Cape area and is not threatened. *L. leimonias* occurs from Aupouri Peninsula (Far North) south to Te Kuiti area and is not threatened either.

All species (except *L. labyrinthica*) intersect in a zone from Taranga Island off eastern Northland south to Te Kuiti including Coromandel Peninsula and islands in Hauraki Gulf.

The species distributions run largely parallel to an extinct subduction zone and the Vening Meinesz transform margin with a distributional gap across the Bay of Plenty (Fig. 14E). This is a standard type of distribution pattern, mapped and discussed in Heads (2017 and references therein) and involves plant and animals such as: *Beilschmiedia* species, NZ tusked weta, rhytidid and charopid snails (e.g., *Chaureopa* species Climo, 1985, Fig. 9 and *Phenacharopa novoseelandica* (Pfeiffer, 1853)). Other invertebrate species relationships between Three Kings Islands and mainland New Zealand were discussed recently by Buckley and Leschen (2013) and Leschen and Buckley (2015).

AUTHORS' CONTRIBUTIONS

FMC did all the original shell morphological analyses, dissections and line drawings of the species discussed and therefore is the author of *Laoma ordishi* Climo n. sp. KM collated all the information and wrote the text with contributions from IP & DJR, and DJR photographed and processed the colour photos presented in this paper.

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