

1 **Radiation and decline of endodontid land**
2 **snails in Makatea, French Polynesia**

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9 Abstract

10 The family Endodontidae Pilsbry, 1895 comprised one of the most diverse
11 groups of indigenous land snails of Pacific Islands. However, due to
12 anthropogenic degradation of their habitats and predation by or competition
13 with introduced species, most members of the family are now extinct or
14 severely endangered. Based on limited and sporadic collections, the
15 endodontid fauna of the raised coral island of Makatea in the western
16 Tuamotu Archipelago was known to consist of four **valid** species,
17 *Mautodontha* (*Mautodontha*) *daedalea* (Gould, 1846), *Kleokyphus callimus*
18 Solem, 1976, *K. hypsus* Solem, 1976 and *Pseudolibera lilliana* Cooke &
19 Solem, 1976, the last three of which endemic. To these, we add eighteen new
20 species based on a reappraisal of museum collections and analysis of
21 abundant new material collected in 2005: *M. (M.) domaneschii*,
22 *M. (M.) virginiae*, *M. (M.) harperae*, *Mautodontha (Garrettoconcha) aurora*,
23 *M. (G.) occidentalis*, *M. (G.) temaoensis*, *M. (G.) makateaensis*, *M. (G.)*
24 *passosi*, *M. (G.) spelunca*, *K. cowiei*, *P. solemi*, *P. matthieui*, *P. cookei*,
25 *P. aubertdelaruei*, *P. extincta*, *P. paraminderae*, *P. elieporoii*, and *P parva*.
26 The recently collected material also revealed new information on the
27 morphology, intraspecific variation and distribution of the four previously
28 known species, which are revised and re-described in this study. With
29 twenty-two recognized taxa, the radiation of endodontids in Makatea is
30 second in species richness only to that of Rapa Iti in the Austral Islands,
31 from where twenty-four endodontids were previously described. Despite
32 intensive field work in Makatea, only *M. (M.) daedalea* was found alive in
33 2005. All other Makatean endodontids were represented solely by empty and
34 worn shells and are possibly extinct.

³⁵ **Keywords:** extinction, endemism, biodiversity, islands, systematics, new
³⁶ species.

37 Introduction

38 Located at 15.85°S and 148.25°W, Makatea is a raised coral atoll in the
39 northwestern part of the Tuamotu Archipelago, French Polynesia (Fig. 1).
40 The island comprises a limestone plateau of approximately 28 km², with a
41 maximum elevation of 113 m, and is surrounded by cliffs ranging from 45 to
42 75 meters in height (Montaggioni & Camoin 1997; Gargominy *et al.* 2006).

43 The pre-european history of Makatea is poorly documented. Only two
44 ancient religious structures (marae) and burial sites in coastal caves **still**
45 **exist** (Verin 1964; Niva 2008), **whereas** Emory (1934) noted, on the basis of
46 oral reports, the former existence of seven other marae on the island.

47 With the discovery of large phosphate deposits around 1890 and their
48 heavy **exploitation** in subsequent years, Makatea became the industrial and
49 business capital of French Polynesia (Beslu 2008). From 1908 to 1966, more
50 than 11 million tons of phosphate were extracted from the atoll by the
51 Compagnie Française des Phosphates de l’Océanie (CFPO), producing
52 thousands of deep pits on approximately one third of the surface of the
53 island (Egretaud & Jouvin 2012). At the peak of the mining activities, the
54 island was inhabited by some 3,000 people (Molet 1964), with an **attendant**
55 infrastructure of railroads, port, hospital, school, restaurants, post office,
56 police station **and** cinemas, among other facilities (Decoudras *et al.* 2005;
57 Beslu 2008). However, with the cessation of mining in 1966, Makatea was
58 almost completely abandoned and only three families remained (Gargominy
59 *et al.* 2006).

60 Makatea is now inhabited by less than one hundred people (population
61 estimated at 61 in 2007; Ghestemme 2013) dedicated to agriculture, fishing
62 and hunting coconut crabs (Lagouy 2007). However, plans for future

63 development, which include secondary mining activities (Egretaud & Jouvin
64 2012) and intensification of tourism (Decoudras *et al.* 2005), may once again
65 alter the dynamics of the atoll.

66 [FIGURE 1 approximately here]

67 During the **years of phosphate mining**, the vegetation of Makatea was
68 altered by clearing of the **mined** area, and by anthropogenic **species**
69 introductions. Butaud & Jacq (2008) reported 403 species of vascular plants
70 present on the atoll, of which 289 are regarded as modern **arrivals** and 43 as
71 pre-european introductions. Of the 71 indigenous species, four are island
72 endemics. Primary forests cover almost three fourths of the surface of
73 Makatea, southwest of the mined area, and concentrate the majority of the
74 indigenous vascular plants (Fig. 2; Butaud & Jacq 2008, table 2, fig. 1).

75 Studies of the land snail fauna of Makatea are few and based on scarce
76 material, most of which from short and opportunistic collections. The
77 earliest documented survey was that of J.P. Couthouy in 1839 during the
78 United States Exploring Expedition. Based on specimens collected by
79 Couthouy, Gould (1846a) prepared the first description of an endodontid
80 species from the island, *Mautodontha (Mautodontha) daedalea*. Cooke (1934)
81 reported on material collected by W.B. Jones in 1922, K.P. Emory in 1930
82 and by G.P. Wilder in 1932, including a single worn specimen of
83 Endodontidae that he hesitated to describe as new; this specimen was
84 subsequently chosen by Solem (1976) as the holotype of a second endodontid
85 snail from Makatea, *Pseudolibera lillianae*. The next documented collection
86 of Makatean land snails was undertaken by the geologist E. Aubert de la
87 Rüe in 1955 (Aubert de la Rüe & Soyer 1958). Using specimens recovered by
88 Aubert de la Rüe, Solem (1976) described two additional species of

89 Endodontidae, *Kleokyphus callimus* and *K. hypsus*. A few years later, Solem
90 (1983) recognized three undescribed species of *Pseudolibera* among Aubert
91 de la Rüe's material, but his early death prevented him from formally
92 describing them.

93 The present study is based on abundant material from an extensive survey
94 of the terrestrial malacofauna of Makatea, conducted in 2005 by two of us
95 (Gargominy *et al.* 2006). It revises the endodontid fauna of the island,
96 describing, illustrating and comparing twenty-two species, eighteen of which
97 are new to science. Most of these species were represented solely by empty
98 and worn shells; only one, *M. (M.) daedalea*, was found alive on Makatea in
99 2005.

100 **Material and Methods**

101 Specimens were collected from twenty-five stations during a malacological
102 survey of Makatea, conducted from 14 to 20 November 2005 (stations
103 Mk01–Mk25; Table 1; Fig. 2). Two methods of collection were used:
104 (1) specimens were located visually and hand picked; (2) samples of soil and
105 leaf litter were sieved through a 1-cm mesh; the residue was then dried and
106 sieved through meshes of 3, 2 and 0.63 mm; material retained by these finer
107 sieves was surveyed for snails, using a stereo-microscope for the fraction
108 between 2 and 0.63 mm. The fraction below 0.63 mm was discarded. All
109 recovered material, including 6515 endodontid specimens, is lodged in the
110 collections of the Muséum national d’Histoire naturelle, Paris (MNHN).

111 [FIGURE 2 approximately here]

112 [Table 1 approximately here]

113 Prior to imaging, specimens were immersed in water, cleaned with fine
114 brushes and air-dried. Stacks of photographs were taken using a digital
115 single-lens reflex camera attached to a stereo-microscope and processed in
116 CombineZP (Hadley 2010) to generate composite images with extended
117 depth of field. Scanning electron microscopy (SEM) was conducted on
118 uncoated material, including holotypes and paratypes. Shell measurements,
119 as well as ribs and whorls counts, were obtained from photographs (Fig. 3).
120 Apertural barriers were numbered according to the system used by Sartori
121 *et al.* (2013): those on the parietal wall counted from the apical to the
122 umbilical suture, and those on the palatal wall in the opposite direction
123 (Fig. 3D). Apertural traces **on the palatal and parietal walls** were counted
124 separately from major barriers.

125

[FIGURE 3 approximately here]

126

Endodontid type specimens in the collection of the Bernice P. Bishop

127

Museum (BPBM) were borrowed and photographed in 2010; types in the

128

Field Museum of Natural History (FMNH) were studied and photographed

129

during a one day visit in November 2012. Photographs of the lectotype of

130

M. (M.) daedalea were kindly provided by Adam Baldinger, Museum of

131

Comparative Zoology (MCZ).

132 **Systematic descriptions**

133 **Order Pulmonata Cuvier in Blainville, 1814**

134 **Suborder Stylommatophora Schmidt, 1855**

135 **Superfamily Punctoidea Morse, 1864**

136 **Family Endodontidae Pilsbry, 1895**

137 **Genus *Mautodontha* Solem, 1976**

138 **Subgenus *Mautodontha* s.s.**

139 *Mautodontha* Solem, 1976: 151. Type species (by original designation):

140 *Helix daedalea* Gould, 1846.

141 ***Mautodontha (Mautodontha) daedalea* (Gould, 1846)**

142 *Helix daedalea* Gould 1846a, p. 173.

143 *Helix daedalea* Gould — Pfeiffer 1848, p. 186.

144 *Helix (Endodonta) daedalea* Gould — Albers 1850, p. 89.

145 *Helix daedalea* Gould — Gould 1852, pp. 54–55.

146 *Helix daedalea* Gould — Gould 1860, p. 4, pl. 4, figs 51,51a–d.

147 *Helix daedalea* Gould — Pfeiffer 1853, p. 144.

148 *Pityx daedalea* (Gould) — Adams & Adams 1858, p. 113.

149 *Helix daedalea* Gould — Pfeiffer 1859, p. 155.

150 *Helix (Endodonta) daedalea* Gould — Albers 1860, p. 90.

151 *Helix daedalea* Gould — Gould 1862, pp. 21–22.

152 *Helix daedalea* Gould — Pfeiffer 1868, p. 221.

153 *Pityx daedalea* (Gould) — Pease 1871, p. 474.

154 *Helix daedalea* Gould — Pfeiffer 1876, p. 258.

155 *Helix (Endodonta) daedalea* Gould — Tryon 1887, p. 64, pl. 12, figs 23–25.

156 *Endodonta (Thaumatodon) daedalea* (Gould) — Pilsbry 1893, p. 27.

157 *Thaumatodon daedalea* (Gould) — Cooke 1934, p. 5.

158 *Endodonta consobrina* (Garrett) — Aubert de la Rüe & Soyer 1958, p. 365, *non*

159 *Pityx consobrina* Garrett 1884.

160 *Helix daedalea* Gould, 1846 — Johnson 1964, p. 65.

161 *Mautodontha (Mautodontha) daedalea* (Gould, 1846) — Solem 1976,
162 pp. 157–158, table 65, figs 73c–d.

163 *Mautodontha daedalea* (Gould, 1846) — Solem 1983, pp. 279–280.

164 Figures 3D; 4; 5; 35A; 37A; 39.

165

166 **Examined material** (2780 specimens). MNHN, unregistered, 11 shells,
167 Tuamotu Islands: Makatea. Collected by E. Aubert de la Rüe in 1955.

168 Determined by Solem; 104 shells, Mk03; 425 shells, Mk04; 135 shells, Mk05;
169 10 shells, Mk06; 23 shells, Mk07; MNHN 25584, 29 specimens preserved in
170 ethanol (21 with soft parts, 8 empty shells), Mk08; 1000 shells, Mk08; 372
171 shells, Mk09; 69 shells, Mk10; 2 shells, Mk11; 15 shells, Mk12; MNHN 25587,
172 1 shell (specimen 9), Mk13; MNHN 25588, 8 shells (specimens 10–17), Mk13;
173 221 shells, Mk13; 24 shell, Mk15; 28 shells, Mk16; 14 shells, Mk17; 13 shells,
174 Mk18; 18 shells, Mk19; 31 shells, Mk20; 45 shells, Mk21; 141 shells, Mk22;
175 41 shells, Mk25.

176 **Type locality:** Matea Islands [= Makatea].

177 **Diagnosis:** Shell less than 4 mm in diameter, discoidal, flammulated,
178 without a supraperipheral groove; teleoconch sculptured by narrow, tall and
179 relatively crowded primary axial ribs (>110 ribs on body whorl); palatal wall
180 with five or six barriers, rarely accompanied by one to three traces; parietal
181 wall with three or four barriers, rarely accompanied by one or two traces.

182 **Description:** Shell discoidal, white to light brown, with maroon
183 flammulations, regularly or irregularly spaced, often fading out on the
184 vicinity of the umbilicus. Shell wall thin, opaque to pellucid; periostracum
185 adherent, shiny. Apex flat to barely raised, spire barely elevated; last whorl
186 descending more rapidly. Apical and umbilical sutures impressed; whorls

187 slightly flattened above periphery or uniformly rounded; periphery rounded
188 to obtusely angled. Transition between protoconch and teleoconch
189 indistinct. Protoconch sculptured by fine axial riblets, initially with
190 interspaces ten to fifteen times their width, undifferentiated; axial riblets
191 progressively differentiating from the third quarter of the first whorl
192 onwards, some increasing in prominence and transitioning into the primary
193 ribs of the teleoconch, others becoming close-set and **wavy**, transitioning into
194 the secondary riblets of the teleoconch. Spiral sculpture of the protoconch
195 comprising approximately equidistant lirae with interspaces four to six times
196 their width, persisting on the surface of the teleoconch. Primary axial
197 sculpture of the teleoconch comprising narrow, tall ribs, with interspaces
198 approximately twelve to fifteen times their width, **extended** by deciduous
199 periostracal lamellae. Secondary axial sculpture of the teleoconch comprising
200 fine, crowded, wavy riblets, with interspaces approximately three to five
201 times their width, **extended** by periostracal lamellae. Umbilicus shallow, V
202 to U-shaped. Peristome crescent-shaped; columellar lip very slightly
203 reflected. Palatal wall usually with five or six barriers, all extending
204 approximately 1/8 whorl, with gradual anterior and abrupt posterior
205 descension, slightly recessed within the aperture; barrier 1 columellar in
206 position, often absent or represented by a trace, often more deeply recessed
207 than remainder; barrier 2 at the confluence of basal and columellar walls,
208 intermediate in prominence between barrier 1 and barriers 3 to 5, similar in
209 prominence to barrier 6; barriers 3 to 5 basal in position, approximately
210 equidistant, similar in prominence; barrier 6 slightly supraperipheral. One to
211 three additional traces rarely present on the palatal wall, variable in
212 position, commonly occurring between barriers 2 and 3, or between barrier 6
213 and apical suture. Parietal wall usually with three or four barriers, with

214 gradual anterior and abrupt posterior descension; barriers 1 to 3 extending
215 approximately 1/8 whorl, similar in prominence, equidistant, not recessed;
216 barrier 4, when present, usually less prominent than remainder, extending
217 approximately 1/8 whorl, not recessed; barrier 4 occasionally trace-like,
218 extending approximately 1/16 whorl, slightly recessed within aperture. One
219 or two additional traces rarely present on the parietal wall, variable in
220 position, commonly occurring between barriers 2 and 3, or between barrier 3
221 and umbilical suture. Other shell features that can be expressed numerically
222 are shown in Table 2.

223 **Remarks:** The deciduous periostracal lamellae projecting from the axial
224 sculpture of the teleoconch were only visible in the few fresh shells and live
225 specimens recovered from station Mk08. These specimens represent the only
226 extant endodontid population we found in Makatea in 2005. Based on
227 material deposited in the Bishop Museum, Solem (1976, p. 158) established
228 that *M. (M.) daedalea* also occurred in the atolls of Anaa and Niau,
229 Tuamotu Archipelago. The presence of the species in Tahiti, Society Islands,
230 was reported by Gould (1852, p. 55) but subsequently challenged by Cooke
231 (1934, p. 5).

232 *M. (M.) daedalea* appears to be rather variable, particularly in the
233 diameter and configuration of its umbilicus, number of apertural barriers,
234 and in the shape of its periphery. The lectotype and most specimens we
235 collected have V-shaped, widely open umbilici (Fig. 4A–B; Table 2,
236 specimens 1–8), but numerous shells display U-shaped umbilici (Fig. 4C–D)
237 that vary in diameter from very wide (Fig. 4C; Table 2, specimens 9–17) to
238 comparatively narrow (Fig. 4D; Table 2, specimens 18–26). Variation in the
239 number of apertural barriers appears to be loosely correlated with
240 differences in the shape of the periphery; specimens with a more angular

241 periphery (Fig. 4B) usually have less barriers than those with the periphery
 242 uniformly rounded (Fig. 4C–D), but numerous exceptions were found among
 243 the studied material.

244 Although isolated specimens may appear separable, intermediates bridging
 245 the gap between morphological extremes were numerous in the samples, and
 246 ultrastructural examination failed to reveal noteworthy differences in
 247 sculpture and protoconch morphology among the three umbilical morphs.
 248 We therefore interpret the observed variability as intraspecific.

249 [FIGURE 4 approximately here]

250 [FIGURE 5 approximately here]

251 *Mautodontha (Mautodontha) domaneschii* sp. nov.

252 Figures 6A; 7; 35B; 37B; 39.

253

254 **Examined material** (744 specimens). **Holotype:** MNHN 25585, Mk04.

255 **Paratypes:** MNHN 25586, 8 shells, Mk04 **Additional material:** 438

256 shells, Mk04; 11 shells, Mk07; 99 shells, Mk08; 187 shells, Mk09;

257 **Type locality:** Moumu cave (15.83347°S; 148.24933°W). Deposits inside
 258 cave. Limestone, alt. 30 m.; station Mk04.

259 **Diagnosis:** Shell less than 3.5 mm in diameter, discoidal, with a shallow
 260 suprapерipheral groove, without flammulations; teleoconch sculptured by
 261 broad, relatively well-spaced primary axial ribs (<90 ribs on body whorl);
 262 umbilicus V-shaped; peristome subovate; palatal wall with four or rarely five
 263 barriers; parietal wall with three or rarely four barriers.

264 **Description:** Shell discoidal, white to fawn, without markings. Shell
265 wall thin, subpellucid to opaque; periostracum adherent, shiny. Apex and
266 spire barely elevated; last whorl descending more rapidly. Apical and
267 umbilical sutures impressed; periphery weakly angled. Whorls flattened
268 above periphery, with a very shallow suprapерipheral groove developing
269 approximately from the middle of the fourth whorl onwards; whorls evenly
270 rounded on basal margin. Transition between protoconch and teleoconch
271 indistinct. Axial sculpture of the protoconch initially comprising pairs of
272 riblets separated by interspaces eight to twelve times the width of an
273 individual riblet; riblets within each pair initially separated by a narrow
274 interspace approximately equal to twice their width, subsequently coming
275 closer and progressively merging into prominent ribs, which comprise the
276 primary sculpture of the teleoconch. Single axial riblets between pairs
277 occurring approximately from the second half of the first whorl,
278 progressively increasing in number and transitioning into the secondary
279 sculpture of the teleoconch. Spiral sculpture of the protoconch comprising
280 approximately equidistant lirae with interspaces five to ten times their
281 width, persisting on the surface of the teleoconch, forming tiny nodules at
282 intersections with the secondary axial sculpture. Teleoconch sculptured by
283 broad axial ribs, with interspaces two to three times their width, slightly
284 taller at periphery than elsewhere, overlaid by wavy axial riblets with
285 interspaces approximately equal to twice their width and by a spiral
286 microsculpture of fine lirae. Umbilicus shallow, V-shaped. Peristome
287 subovate. Palatal barriers usually four, rarely five, extending approximately
288 1/8 whorl, with gradual anterior and abrupt posterior descension, regularly
289 spaced, slightly recessed; barrier 1 at the confluence of basal and columellar
290 walls; barriers 2 and 3 basal, barrier 5 suprapерipheral; barrier 4, when

291 present, positioned approximately midway between barriers 3 and 5; barriers
292 1, 4 and 5 slightly to markedly less prominent than barriers 2 and 3.

293 Parietal barriers usually three, rarely four, extending approximately 3/16
294 whorl, with gradual anterior and abrupt posterior descension, not recessed,
295 taller along the posterior third; barriers 1 and 2 more prominent than barrier
296 3, or barrier 1 more prominent than barriers 2, 3 and 4. Other shell features
297 that can be expressed numerically are shown in Table 2.

298 **Remarks:** The combination of a wide, V-shaped umbilicus with a shallow
299 suprapерipheral groove immediately separates *M. (M.) domaneschii* from all
300 other endodontids of Makatea. *M. (M.) ceuthma* (Solem, 1976), from
301 Raivavae, Austral Islands, is the only previously known species of the genus
302 with a suprapерipheral groove, but that species is quite distinct from
303 *M. (M.) domaneschii*, exhibiting a relatively higher shell and more numerous
304 and prominent apertural barriers.

305 **Etymology:** This species is dedicated to the late Osmar Domaneschi,
306 malacologist and fabulous teacher.

307 [FIGURE 6 approximately here]

308 [FIGURE 7 approximately here]

309 *Mautodontha (Mautodontha) virginiae* sp. nov.

310 Figures 6B; 8; 35C; 37B; 39.

311

312 **Examined material** (167 specimens). **Holotype:** MNHN 25681, Mk19.

313 **Paratypes:** MNHN 25682, 8 shells, Mk19. **Additional material:** 156
314 shells, Mk19; MNHN 25686, 1 shell, Mk18; 1 shell, Mk18.

315 **Type locality:** Coastal cliff north of Moumu (15.81782°S; 148.25673°W).
316 Accumulation zone in rocky substratum. Limestone, alt. 10 m.; station
317 Mk19.

318 **Diagnosis:** Shell less than 4 mm in diameter, depressed, flammulated;
319 teleoconch sculptured by broad, relatively well-spaced primary axial ribs
320 (<110 ribs on body wall); umbilicus V-shaped; palatal wall with five
321 barriers, the first often trace-like; parietal wall with three barriers, rarely
322 accompanied by two traces.

323 **Description:** Shell depressed, white to fawn, with regular spaced, amber
324 flammulations persisting on shell base or fading out in the vicinity of the
325 umbilical margin. Shell wall thin, opaque to pellucid; periostracum
326 adherent, shiny. Apex barely raised, spire elevated; later whorls descending
327 more rapidly. Apical and umbilical sutures impressed; whorls slightly
328 flattened above rounded periphery; obtusely angled at the confluence of
329 basal and columellar walls. Transition between protoconch and teleoconch
330 indistinct. Protoconch sculptured by fine axial riblets, initially with
331 interspaces eight to twelve times their width, becoming progressively
332 crowded, transitioning into the secondary sculpture of the teleoconch. Spiral
333 sculpture of the protoconch comprising lirae with interspaces three to six
334 times their width, persisting on the surface of the teleoconch, forming tiny
335 nodules at intersections with the secondary axial sculpture. Primary axial
336 sculpture of the teleoconch comprising broad, prominent ribs, with
337 interspaces approximately three to four times their width, overlaid by a
338 secondary axial sculpture of fine, crowded, wavy riblets, with interspaces
339 approximately twice to three times their width. Umbilicus deep, V-shaped.
340 Peristome crescent-shaped; columellar lip very slightly reflected. Palatal wall
341 with five barriers, all extending approximately 1/8 whorl, with gradual

342 anterior and posterior descension, approximately equidistant, recessed within
343 the aperture; barrier 1 columellar in position, often trace-like; barriers 2 to 5
344 basal in position; barriers 3 and 4 slightly more prominent and less recessed
345 than remainder. Parietal wall with three barriers and, rarely, two traces; all
346 parietal barriers extending approximately 3/16 whorl, with gradual anterior
347 and posterior descension, not recessed within the aperture, approximately
348 equidistant, similar in prominence. Trace 1 positioned between barriers 1
349 and 2; trace 2 between barriers 2 and 3. Other shell features that can be
350 expressed numerically are shown in Table 2.

351 **Remarks:** One of the specimens recovered from station Mk18 has the
352 whorls much flattened below the periphery and four parietal barriers
353 (Fig. 8E). Although it appears separable from typical *M. (M.) virginiae*,
354 ultrastructural examination failed to reveal any differences in the protoconch
355 or teleoconch sculpture. Hence, in the absence of additional individuals
356 displaying such morphology, we see this specimen as an aberrant
357 *M. (M.) virginiae*. Additional field efforts at and around Mk18 are needed to
358 re-evaluate this hypothesis.

359 In body size, coloration and shell shape, *M. (M.) virginiae* somewhat
360 resembles *M. (M.) daedalea*, from which it is easily distinguished by its
361 coarser and less dense primary ornamentation (Table 2), higher spire and a
362 more abrupt transition between the columellar and basal margins of the
363 aperture. The relatively coarse ornamentation of *M. (M.) virginiae* also aids
364 its distinction from *M. (M.) harperae* sp. nov., which has a similar general
365 shape and body size but bears much finer sculpture and more prominent
366 aperture barriers; in addition, *M. (M.) harperae* is not known to display
367 flammulations. A wider umbilicus provides the easiest criterion for
368 separating *M. (M.) virginiae* from the seemingly further related *Mautodontha*

369 (*Garrettoconcha*) *aurora* sp. nov. and *Kleokyphus cowiei* sp. nov.

370 **Etymology:** This species is dedicated to our colleague Virginie Héros,
371 curator of Mollusks at the Muséum National d'Histoire Naturelle, for her
372 continuous support.

373 [FIGURE 8 approximately here]

374 *Mautodontha* (*Mautodontha*) *harperae* sp. nov.

375 Figures 6C; 9; 35E; 37C; 39.

376

377 **Examined material** (7 specimens). **Holotype:** MNHN 26529, Mk04.

378 **Paratypes:** MNHN 26530, 6 shells, Mk04

379 **Type locality:** Moumu cave (15.83347°S; 148.24933°W). Deposits inside
380 cave. Limestone, alt. 30 m.; station Mk04.

381 **Diagnosis:** Shell less than 4 mm in diameter, depressed, without
382 flammulations; teleoconch sculptured by narrow, tall and relatively crowded
383 primary axial ribs (>120 ribs on body wall); umbilicus V-shaped; palatal
384 wall with five barriers, the first more prominent than remainder, rarely
385 accompanied by three traces; parietal wall with three or rarely four
386 conspicuous barriers.

387 **Description:** Shell depressed, white, without flammulations. Shell wall
388 thin, subpellucid; periostracum adherent, shiny. Apex flat to barely raised,
389 spire elevated; later whorls descending more rapidly. Apical and umbilical
390 sutures impressed; whorls and periphery rounded; basal and columellar walls
391 transitioning smoothly. Transition between protoconch and teleoconch
392 indistinct. Axial sculpture of the protoconch initially comprising pairs of fine
393 riblets separated by interspaces eight to ten times the width of an individual

394 riblet; riblets within each pair initially separated by a narrow interspace
395 approximately equal to twice their width, subsequently coming closer and
396 progressively merging into prominent ribs, which comprise the primary
397 sculpture of the teleoconch. Single axial riblets between pairs occurring
398 approximately from the second quarter of the first whorl, progressively
399 increasing in number and transitioning into the secondary sculpture of the
400 teleoconch. Spiral sculpture of the protoconch comprising approximately
401 equidistant lirae with interspaces two to three times their width, persisting
402 on the surface of the teleoconch, forming tiny nodules at intersections with
403 the secondary axial sculpture.¹ Umbilicus deep, V-shaped. Peristome
404 crescent-shaped; columellar lip very slightly reflected. Palatal wall with five
405 barriers and, rarely, three traces; all palatal barriers extending
406 approximately 1/8 whorl, with gradual anterior and posterior descension,
407 approximately equidistant; barrier 1 columellar in position, not recessed
408 within the aperture, more prominent than remainder; barriers 2 to 4 basal in
409 position, slightly recessed within the aperture, slightly more prominent than
410 barrier 5; barrier 5 suprapерipheral, deeply recessed. Palatal traces, when
411 present, positioned between barriers 1 and 2, 2 and 3, 3 and 4, more deeply
412 recessed and less prominent than barriers. Parietal wall with three or rarely
413 four conspicuous barriers, all extending beyond the line of vision from the
414 peristome, with abrupt anterior descension, not recessed within the aperture,
415 approximately equidistant. Barriers 2 and 3 more prominent than barrier 1.
416 Barrier 4, when present, less prominent than remainder. Other shell features
417 that can be expressed numerically are shown in Table 2.

418 **Remarks:** The very prominent parietal and columellar barriers of this

¹Note to editor/reviewers: Description of the sculpture of this species will be revisited during revision of the manuscript, when SEMs will be available.

419 species sets it apart from all other endodontids of Makatea. The only
 420 previously known species of *Mautodontha* Solem, 1976 with comparable
 421 parietals and columellar is *M. (M.) ceuthma*, from Raivavae, Austral Islands,
 422 which is easily distinguished from *M. (M.) harperae* by its supraperipheral
 423 groove and more spaced sculpture.

424 **Etymology:** This species is dedicated to Liz Harper, distinguished
 425 malacologist and palaeontologist.

426 [FIGURE 9 approximately here]

427 **Subgenus *Garrettoconcha* Solem, 1976**

428 *Garrettoconcha* Solem, 1976: 162. Type species (by original designation):

429 *Helix parvidens* Pease, 1861.

430 ***Mautodontha (Garrettoconcha) aurora* sp. nov.**

431 Figures 10A; 11; 35F; 38B; 39.

432

433 **Examined material** (234 specimens). **Holotype:** MNHN 25575, Mk22.

434 **Paratypes:** MNHN 25576, 2 shells, Mk22; MNHN 25577, 6 shells, Mk04.

435 **Additional material:** 201 shells, Mk04; 18 shell, Mk19; 6 shells, Mk20.

436 **Type locality:** Plateau west of Anapoto (15.83987°S; 148.22852°W).

437 Karst (feo) on top of cliff with *Ficus* sp. and *Pandanus* sp. Limestone, alt.

438 75 m.; station Mk22.

439 **Diagnosis:** Shell less than 3.5 mm in diameter, depressed, without
 440 flammulations; teleoconch sculptured by narrow, tall and relatively crowded
 441 primary axial ribs (>110 ribs on body wall); umbilicus U-shaped; palatal
 442 wall with five barriers; parietal wall with three barriers.

443 **Description:** Shell depressed, white to fawn, without markings. Shell

444 wall thin, opaque to subpellucid; periostracum adherent, shiny. Apex and
445 spire elevated; later whorls descending more rapidly. Apical and umbilical
446 sutures impressed; whorls and periphery rounded; basal and columellar walls
447 transitioning smoothly. Transition between protoconch and teleoconch
448 indistinct. Axial sculpture of the protoconch initially comprising pairs of fine
449 riblets separated by interspaces eight to twelve times the width of an
450 individual riblet; riblets within each pair initially separated by an interspace
451 three to four times their width, subsequently coming closer and progressively
452 merging into prominent ribs, which comprise the primary sculpture of the
453 teleoconch. Single axial riblets between pairs occurring approximately from
454 the second half of the first whorl, progressively increasing in number and
455 transitioning into the secondary sculpture of the teleoconch. Spiral sculpture
456 of the protoconch comprising approximately equidistant lirae with
457 interspaces six to eight times their width, fading out approximately at the
458 end of the first whorl. Teleoconch sculptured by narrow, tall, prominent
459 axial ribs, with interspaces three to four times their width, overlaid by a
460 secondary ornament of crowded axial riblets, with interspaces approximately
461 equal to their width. Teleoconch devoid of spiral sculpture. Umbilicus deep,
462 U-shaped. Peristome crescent-shaped; columellar lip very slightly reflected.
463 Palatal wall with five barriers, all extending approximately $1/8$ whorl, with
464 gradual anterior and somewhat abrupt posterior descension, regularly spaced
465 and slightly recessed within the aperture; barrier 1 columellar, 2 and 3 basal,
466 4 infraperipheral and 5 peripheral in position; barrier 5 slightly more deeply
467 recessed and usually less prominent than barrier 4. Parietal barriers three,
468 extending approximately $3/16$ whorl, with gradual anterior and abrupt
469 posterior descension, similar in prominence, regularly spaced, not recessed
470 within the aperture. Other shell features that can be expressed numerically

471 are shown in Table 2.

472 **Remarks:** A much larger shell at the same whorl count in *M. (G.) aurora*
 473 provides the best criterion for distinguishing this species from *M. (G.)*
 474 *occidentalis* sp. nov.; other differences include slightly less crowded sculpture,
 475 smoother transition between basal and columellar walls, lower peristome,
 476 and usually a less elevated spire in *M. (G.) aurora*. In general shell shape,
 477 *M. (G.) aurora* resembles *M. (M.) virginiae* and *M. (M.) harperae*, but it is
 478 easily distinguished from those species by its narrower, U-shaped umbilicus.

479 **Etymology:** From *aurora* (latin), meaning sunrise, alluding to the
 480 distribution of this species, which is only known from the eastern coast of
 481 Makatea.

482 [FIGURE 10 approximately here]

483 [FIGURE 11 approximately here]

484 *Mautodontha (Garrettoconcha) occidentalis* sp. nov.

485 Figures 10B; 12; 35D; 37B; 39.

486

487 **Examined material** (32 specimens). **Holotype:** MNHN 25573, Mk13.

488 **Paratypes:** MNHN 25574, 8 shells, Mk13. **Additional material:** 13
 489 shells, Mk13; 2 shell, Mk11; 1 shell, Mk12; 1 shell, Mk15; 6 shells, Mk16.

490 **Type locality:** West coast, approximately 3 km south of Temao
 491 (15.85189°S; 148.28018°W). Cave. Limestone, alt. 10 m.; station Mk13.

492 **Diagnosis:** Shell less than 3 mm in diameter, subdepressed, without
 493 flammulations; teleoconch sculptured by narrow, low and relatively crowded

494 primary axial ribs (>110 ribs on body wall); umbilicus U-shaped; palatal
495 wall with five barriers, the first often trace-like; parietal wall with three
496 barriers.

497 **Description:** Shell subdepressed, white to light fawn, without markings.
498 Shell wall thin, usually opaque, seldom subpellucid; periostracum adherent,
499 shiny. Apex and spire elevated to strongly elevated; later whorls descending
500 more rapidly. Apical and umbilical sutures impressed; whorls sharply
501 rounded apically, broadly rounded along periphery and shell base; confluence
502 of basal and columellar walls usually marked by a tighter curvature.
503 Transition between protoconch and teleoconch poorly marked, at
504 approximately one whorl and a quarter. Axial sculpture of the protoconch
505 comprising pairs of fine riblets separated by interspaces ten to fifteen times
506 the width of an individual riblet; riblets within each pair separated by a
507 narrow interspace equivalent to or twice their width. Spiral sculpture of the
508 protoconch comprising approximately equidistant lirae with interspaces six
509 to eight times their width, fading out approximately at the end of the first
510 whorl. Axial sculpture of the protoconch gradually transitioning into low
511 ribs, with interspaces four to six times their width, which comprise the
512 primary sculpture of the teleoconch. Secondary sculpture of the teleoconch
513 comprised by fine axial riblets occupying the interspaces between primary
514 ribs; riblets initially well-spaced, two to four between each pair of ribs,
515 crowded from the third whorl onwards, commonly with eight to ten riblets
516 between each pair of primary ribs. Teleoconch devoid of spiral sculpture.
517 Umbilicus very deep, U-shaped. Peristome crescent-shaped; columellar lip
518 slightly reflected. Palatal wall with five barriers, all extending approximately
519 1/8 whorl, with somewhat abrupt anterior and posterior descension,
520 regularly spaced and slightly recessed within the aperture; barrier 1

521 columellar in position, often trace-like and attaining only half of the
522 prominence of barrier 2; barriers 2 and 3 basal, 4 infraperipheral and 5
523 peripheral in position; barrier 5 slightly more deeply recessed and less
524 prominent than barrier 4. Parietal barriers three, extending approximately
525 3/16 whorl, with gradual anterior and abrupt posterior descension, similar in
526 prominence, more or less regularly spaced, not recessed within the aperture.
527 Other shell features that can be expressed numerically are shown in Table 2.

528 **Remarks:** *M. (G.) occidentalis* is the smallest endodontid recorded from
529 Makatea (Fig. 35); although the recovered specimens of *M. (G.) temaoensis*
530 sp. nov. are only slightly larger, both display less than 5 whorls and are
531 quite possibly subadults. *M. (G.) occidentalis* is somewhat variable in spire
532 elevation and specimens with a lower spire approach the general shell shape
533 of *M. (G.) aurora*; a higher peristome, less broadly rounded transition
534 between basal and columellar walls, and slightly more crowded sculpture in
535 *M. (G.) occidentalis* are, in addition to the smaller shell size, criteria for
536 distinguishing these species.

537 **Etymology:** From *occidentalis* (latin), alluding to the distribution of this
538 species, which is only known from the western coast of Makatea.

539 [FIGURE 12 approximately here]

540 ***Mautodontha (Garrettoconcha) temaoensis* sp. nov.**

541 Figures 10C; 13; 35H; 37E; 39.

542

543 **Examined material** (19 specimens). **Holotype:** MNHN 25685, Mk16.

544 **Paratypes:** MNHN 26533, 8 shells, Mk16. **Additional material:** 10

545 shells, Mk16.

546 **Type locality:** Road descending to Temoa (15.82593°S; 148.27534°W).

547 Lower side of the road below rocks. Limestone, alt. 10 m.; station Mk16.

548 **Diagnosis:** Shell less than 3 mm in diameter, depressed, without
549 flammulations; teleoconch sculptured by broad, relatively well-spaced
550 primary axial ribs (<90 ribs on body wall); umbilicus V-shaped; palatal wall
551 with four barriers; parietal wall with three conspicuous barriers.

552 **Description:** Shell depressed, white, without markings. Shell wall thin,
553 opaque; periostracum not seen. Apex and spire elevated; later whorls
554 descending slightly more rapidly. Apical and umbilical sutures impressed;
555 whorls flattened above rounded periphery and at columellar wall. Sculpture
556 of protoconch and transition with teleoconch unknown. Primary axial
557 sculpture of the teleoconch comprising broad, prominent ribs, with
558 interspaces approximately three to four times their width, overlaid by a
559 secondary axial sculpture of fine riblets, with interspaces approximately
560 equal to three times their width. Umbilicus deep, V-shaped. Peristome
561 subovate; columellar lip very slightly reflected. Palatal wall with four
562 barriers, all extending approximately 1/8 whorl, with gradual anterior and
563 somewhat abrupt posterior descension, approximately equidistant, recessed
564 within the aperture; barrier 1 columellar or positioned at the confluence of
565 basal and columellar walls; barriers 2 to 4 basal in position; barriers 1 and 4
566 slightly less prominent and more deeply recessed than barriers 2 and 3.
567 Parietal wall with three conspicuous barriers, all extending approximately
568 3/16 whorl, with somewhat abrupt anterior and gradual posterior descension,
569 not recessed within the aperture, similar in prominence; interspace between
570 barriers 1 and 2 slightly larger than interspace between 2 and 3. Other shell
571 features that can be expressed numerically are shown in Table 2.

572 **Remarks:** *M. (G.) temaoensis* was represented in the samples by two

573 worn specimens. Hence, fine details of its sculpture are unknown. It
 574 resembles *M. (G.) occidentalis* in shell size but at a lower whorl count. Its
 575 raised, somewhat pointed apex resembles those of *M. (G.) makateaensis* sp.
 576 nov. and *M. (G.) passosi* sp. nov., from which it differs in having more
 577 numerous aperture barriers, a less elevated spire, and a smaller size at the
 578 same whorl count. A subovate periostome and well-spaced primary sculpture
 579 are additional characters suggesting a close relationship between
 580 *M. (G.) temaoensis* and *M. (G.) makateaensis*.

581 **Etymology:** From the port of Temao. This species is only known from
 582 the road descending to the port.

583 [FIGURE 13 approximately here]

584 *Mautodontha (Garrettoconcha) makateaensis* sp. nov.

585 Figures 14A; 15; 35G; 38B; 39.

586

587 **Examined material** (19 specimens). **Holotype:** MNHN 25683, Mk12.

588 **Paratypes:** MNHN 25684, 8 shells, Mk12. **Additional material:** 10
 589 shells, Mk12.

590 **Type locality:** Approximately 1 km. north of Temao port (15.81638°S;
 591 148.27639°W). Large fault in the cliff, shaded. Ferns. Limestone, alt. 10 m.;
 592 station Mk12.

593 **Diagnosis:** Shell less than 4 mm in diameter, subdepressed, without
 594 flammulations; teleoconch sculptured by narrow, tall, relatively well-spaced
 595 primary axial ribs (<90 ribs on body wall); umbilicus V-shaped; palatal wall
 596 with three barriers; parietal wall with two barriers, rarely accompanied by
 597 two traces.

598 **Description:** Shell subdepressed, white, without markings. Shell wall
599 thin, opaque to pellucid; periostracum adherent, shiny. Apex and spire
600 strongly elevated; later whorls descending slightly more rapidly. Apical and
601 umbilical sutures impressed; whorls and periphery uniformly rounded; basal
602 and columellar walls transitioning smoothly. Transition between protoconch
603 and teleoconch indistinct. Axial sculpture of the protoconch initially
604 comprising pairs of fine riblets separated by interspaces ten to fifteen times
605 the width of an individual riblet; riblets within each pair initially separated
606 by a narrow interspace equivalent to or twice their width, subsequently
607 coming closer and progressively merging into prominent ribs, which comprise
608 the primary sculpture of the teleoconch. Single axial riblets between pairs
609 occurring approximately from the second half of the first whorl, progressively
610 increasing in number and transitioning into the secondary sculpture of the
611 teleoconch. Spiral sculpture of the protoconch comprising lirae with
612 interspaces three to six times their width, fading out approximately on the
613 second half of the second whorl. Teleoconch sculptured by tall, narrow,
614 prominent axial ribs, with interspaces four to five times their width, overlaid
615 by a secondary ornament of crowded axial riblets, with interspaces
616 approximately three to four times their width. Teleoconch devoid of spiral
617 sculpture approximately from the third whorl onwards. Umbilicus very deep,
618 V-shaped. Peristome subovate; columellar lip slightly reflected. Palatal wall
619 with three barriers, all basal in position, extending approximately 1/8 whorl,
620 with gradual anterior descension, similar in prominence, approximately
621 equidistant, slightly recessed within the aperture; posterior descension of
622 barriers 1 and 2 gradual, that of barrier 3 abrupt. Parietal wall with two
623 barriers, both extending approximately 3/16 whorl, with gradual anterior
624 and posterior descension, similar in prominence, taller than palatal barriers,

625 not recessed within the aperture. Rarely with one trace between parietal
626 barriers and one trace between parietal barrier 2 and umbilical suture. Other
627 shell features that can be expressed numerically are shown in Table 2.

628 **Remarks:** Little intraspecific variation is observable in our sample of this
629 species, all recovered specimens being very similar to the holotype. The
630 pattern of two parietal and three palatal barriers is, together with a larger
631 shell at the same whorl count, the easiest **critierion** for distinguishing this
632 species from *M. (G.) temaoensis*. Only *M. (G.) passosi* sp. nov. and *M. (G.)*
633 *spelunca* sp. nov. are also characterized by two parietal barriers; both may
634 be distinguished from *M. (G.) makateaensis* by their more closely-set
635 sculpture.

636 **Etymology:** From Makatea.

637 [FIGURE 14 approximately here]

638 [FIGURE 15 approximately here]

639 *Mautodontha (Garrettoconcha) passosi* sp. nov.

640 Figures 14B; 16; 35J; 37E; 39.

641

642 **Examined material** (146 specimens). **Holotype:** MNHN 25578, Mk19.

643 **Paratypes:** MNHN 25579, 8 shells, Mk19. **Additional material:** 136
644 shells, Mk19; 1 shell, Mk04.

645 **Type locality:** Coastal cliff north of Moumu (15.81782°S; 148.25673°W).

646 Accumulation zone in rocky substratum. Limestone, alt. 10 m.; station

647 Mk19.

648 **Diagnosis:** Shell less than 4 mm in diameter, subdepressed, without
649 flammulations; teleoconch sculptured by narrow, tall, relatively crowded
650 primary axial ribs (>80 ribs on body wall); umbilicus U-shaped; palatal wall
651 with four low barriers; parietal wall with two barriers.

652 **Description:** Shell subdepressed, white, without markings. Shell wall
653 thin, opaque; periostracum adherent, matt. Apex and spire strongly
654 elevated; later whorls descending more rapidly. Apical and umbilical sutures
655 impressed; whorls and periphery rounded; columellar wall somewhat
656 flattened. Transition between protoconch and teleoconch indistinct. Axial
657 sculpture of the protoconch initially comprising pairs of fine riblets
658 separated by interspaces ten to fifteen times the width of an individual
659 riblet; riblets within each pair initially separated by a narrow interspace two
660 to three times their width, subsequently coming closer and progressively
661 merging into narrow, tall ribs, which comprise the primary sculpture of the
662 teleoconch. Single axial riblets between pairs occurring approximately from
663 the second quarter of the first whorl, progressively increasing in number and
664 transitioning into the secondary sculpture of the teleoconch. Spiral sculpture
665 of the protoconch comprising approximately equidistant lirae with
666 interspaces three to five times their width, persisting on the surface of the
667 teleoconch, forming tiny nodules at intersections with the secondary axial
668 sculpture. Umbilicus very deep, U-shaped. Peristome crescent-shaped;
669 columellar lip slightly reflected. Palatal wall with four low barriers, all
670 extending approximately 1/8 whorl, with gradual anterior and posterior
671 descension, regularly spaced and slightly recessed within the aperture;
672 barrier 1 columellar in position; barriers 2 to 4 basal. Parietal wall with two
673 barriers, both extending approximately 1/8 whorl, with somewhat abrupt
674 anterior and gradual posterior descension, similar in prominence, taller than

675 palatal barriers, not recessed within the aperture. Other shell features that
 676 can be expressed numerically are shown in Table 2.

677 **Remarks:** *M. (G.) passosi* is similar to *M. (G.) makateaensis* and *M.*
 678 *(G.) spelunca* sp. nov. in the presence of two parietal barriers, but differs
 679 from both in bearing four palatals. Additionally, from *M. (G.) makateaensis*
 680 it differs in exhibiting more closely-set sculpture and usually a slightly higher
 681 spire; and from *M. (G.) spelunca* by a smaller shell at the same whorl count.

682 **Etymology:** This species is dedicated to Fávio Dias Passos, who
 683 introduced the first author to malacology.

684 [FIGURE 16 approximately here]

685 ***Mautodontha (Garrettoconcha) spelunca* sp. nov.**

686 Figures 3A–C; 14C; 17; 35I; 37C; 39.

687

688 **Examined material** (207 specimens). **Holotype:** MNHN 25582, Mk13.

689 **Paratypes:** MNHN 25583, 8 shells, Mk13. **Additional material:** 198
 690 shells, Mk13.

691 **Type locality:** West coast, approximately 3 km south of Temao
 692 (15.85189°S; 148.28018°W). Cave. Limestone, alt. 10 m.; station Mk13.

693 **Diagnosis:** Shell less than 5 mm in diameter, depressed, without
 694 flammulations; teleoconch sculptured by narrow, tall, relatively crowded
 695 primary axial ribs (>90 ribs on body wall); umbilicus V-shaped; palatal wall
 696 with three or occasionally two low barriers; parietal wall with two
 697 conspicuous barriers, occasionally accompanied by one trace.

698 **Description:** Shell depressed, white, without markings. Shell wall thin,
 699 pellucid; periostracum adherent, shiny. Apex and spire elevated; later whorls

700 descending more rapidly. Apical and umbilical sutures impressed; whorls
701 rounded to very slightly flattened above periphery; basal wall uniformly
702 rounded, columellar wall broadly rounded, their confluence usually marked
703 by a tighter curvature. Transition between protoconch and teleoconch
704 indistinct. Axial sculpture of the protoconch initially comprising pairs of fine
705 riblets separated by interspaces eight to twelve times the width of an
706 individual riblet; riblets within each pair initially separated by a narrow
707 interspace approximately equal to twice their width, subsequently coming
708 closer and progressively merging into prominent ribs, which comprise the
709 primary sculpture of the teleoconch. Single axial riblets between pairs
710 occurring approximately from the second quarter of the first whorl onwards,
711 progressively increasing in number and transitioning into the secondary
712 sculpture of the teleoconch. Spiral sculpture of the protoconch comprising
713 approximately equidistant lirae with interspaces three to four times their
714 width, fading out approximately on the first quarter of the second whorl.
715 Teleoconch sculptured by tall, narrow axial ribs, with interspaces three to
716 four times their width, overlaid by a secondary ornament of riblets, with
717 interspaces approximately three to six times their width. Teleoconch devoid
718 of spiral sculpture. Umbilicus deep, V-shaped. Peristome crescent-shaped;
719 columellar lip slightly reflected. Palatal wall usually with three low barriers,
720 all extending approximately 1/16 whorl, with abrupt anterior and posterior
721 descension, recessed within the aperture; barrier 1 at the confluence of basal
722 and columellar walls, commonly trace-like, occasionally lacking, slightly
723 more deeply recessed than remainder; barriers 2 and 3 basal in position,
724 similar in prominence, with an interspace slightly smaller than that between
725 barriers 1 and 2. Parietal wall with two prominent barriers, both extending
726 approximately 1/8 whorl, with abrupt anterior and posterior descension, not

727 recessed within the aperture, similar in prominence. One parietal trace
 728 occasionally present between the barriers. Other shell features that can be
 729 expressed numerically are shown in Table 2.

730 **Remarks:** *M. (G.) spelunca* is similar to *M. (G.) makateaensis* in the
 731 presence of three palatals and two parietals, but differs from that species in
 732 its larger shell size, more closely-set sculpture and usually wider umbilicus.
 733 *M. (G.) spelunca* is also larger and usually has a wider umbilicus than *M.*
 734 *(G.) passosi*, from which it is additionally distinguished by bearing three
 735 rather than four palatal barriers.

736 **Etymology:** From *spelunca* (latin), meaning cave. This species is only
 737 known from a cave in the west coast of Makatea.

738 [FIGURE 17 approximately here]

739 **Genus *Kleokyphus* Solem, 1976**

740 *Kleokyphus* Solem, 1976: 224. Type species (by original designation):

741 *Kleokyphus callimus* Solem, 1976.

742

743 ***Kleokyphus callimus* Solem, 1976**

744 *Libera heynemanni* (Pfeiffer) — Aubert de la Rüe & Soyer 1958, p. 365, *non*

745 *Helix heynemanni* Pfeiffer 1862.

746 *Kleokyphus callimus* Solem 1976, pp. 224–226, table 75, figs 95a–c

747 Figures 18; 19; 35K; 37D; 39.

748

749 **Examined material** (10 specimens). **Holotype:** MNHN. Tuamotu
 750 Islands: Makatea. Collected by E. Aubert de la Rüe in 1955. **Paratypes:**

751 MNHN, 1 shell, from the type locality. FMNH 153781, 2 shells, from the
752 type locality. **Additional material:** MNHN 25570, 6 shells, Mk16.

753 **Diagnosis:** Shell less than 5 mm in diameter, depressed, flammulated;
754 apical suture adpressed; teleoconch sculptured by narrow, very low,
755 relatively crowded primary axial ribs (>90 ribs on body wall); umbilicus
756 U-shaped, slightly constricted at last whorl; palatal wall with six barriers
757 and two traces; parietal wall with four barriers and one trace, rarely with
758 three barriers and three traces.

759 **Type locality:** Tuamotu Islands: Makatea. Collected by E. Aubert de la
760 Rüe in 1955.

761 **Description:** Shell depressed, white, with regularly spaced, amber
762 flammulations fading out on the shell base. Shell wall thin, opaque;
763 periostracum adherent, matt. Apex flat, spire elevated; whorls descending
764 progressively more rapidly. Periphery slightly angulated; supraperipheral
765 wall broadly convex; infraperipheral wall rounded, smoothly transitioning
766 into basal and columellar walls. Apical suture adpressed, umbilical suture
767 impressed. Transition between protoconch and teleoconch indistinct.
768 Sculpture of the first whorl unknown; second whorl ornamented by narrow
769 axial riblets, with interspaces six to eight times their width. From the third
770 whorl onwards, primary sculpture comprised by very low, relatively wide
771 axial ribs, with interspaces three to eight times their width, more prominent
772 on the shell base than apically; primary ribs overlaid by a secondary axial
773 sculpture of crowded, very low, wavy riblets, with interspaces approximately
774 one fifth to half of their width, and by minute spiral cords. Umbilicus very
775 deep, U-shaped, slightly wider apically than at last whorl. Peristome
776 crescent-shaped; columellar lip slightly reflected. Palatal wall with two
777 traces and six barriers; traces slightly recessed within aperture, very low;

778 trace 1 columellar, extending inward beyond the line of vision from the
779 peristome; trace 2 just below apical suture, extending approximately 1/8
780 whorl; palatal barriers approximately equidistant along infraperipheral,
781 basal and columellar walls; barriers 1, 2 and 6 slightly recessed; barriers 1
782 and 6 less prominent than remainder; barrier 1 columellar, with gradual
783 anterior descension, extending inward beyond the line of vision from the
784 peristome; barriers 2 to 6 extending approximately 1/8 whorl, with gradual
785 anterior and posterior descension; barriers 2 to 5 not recessed, similar in
786 prominence. Parietal wall usually with one trace and four barriers, rarely
787 with three traces and three barriers; trace 1 just below apical suture,
788 extending inward beyond the line of vision from the peristome, very low;
789 barriers approximately equidistant, extending 1/8 whorl, not recessed, with
790 gradual anterior and posterior descension; barriers 1 to 3 similar in
791 prominence, slightly taller than barrier 4; barrier 4 rarely absent and
792 replaced by two close-set, low additional traces, not recessed within aperture
793 and extending 1/16 whorl. Other shell features that can be expressed
794 numerically are shown in Table 2.

795 **Remarks:** Solem (1976) established *K. callimus* based on four specimens
796 collected by Aubert de la Rüe from Makatea, without more precise locality
797 data. To these, we add six specimens recovered from station Mk16, bringing
798 the number of known individuals to ten. All agree well with the original
799 description. The holotype, figured here for the first time (Fig. 18A), is a
800 small adult specimen with the sculpture comparatively well-preserved but
801 missing part of the palatal wall and barriers. The largest of the paratypes
802 lodged in the Field Museum shows the feeble spiral cording of the species
803 more clearly than any other specimen (Fig. 19E). Specimen 1 of our series
804 has two close-set traces in place of the fourth parietal barrier (Fig. 19F).

805 Intraspecific variation in other features seems small and not noteworthy.
 806 *K. callimus* is the type species of *Kleokyphus* Solem, 1976 and the only
 807 representative of the genus displaying a shallow, adpressed apical suture,
 808 and the sculpture greatly reduced above the periphery.

809 [FIGURE 18 approximately here]

810 [FIGURE 19 approximately here]

811 ***Kleokyphus hypsus* Solem, 1976**

812 *Libera gregaria* Garrett — Aubert de la Rüe & Soyer 1958, p. 365, *non Libera*
 813 *gregaria* Garrett 1884.

814 *Kleokyphus hypsus* Solem 1976, pp. 226–227, table 75, figs 95d–f.

815 Figures 20A–C; 21; 35L; 37D; 39.

816

817 **Examined material** (327 specimens). **Holotype**: MNHN 25571.

818 Tuamotu Islands: Makatea. Collected by E. Aubert de la Rüe in 1955.

819 **Additional material**: 1 shell, Mk12; MNHN 25572, 325 shells, Mk19.

820 **Type locality**: Tuamotu Islands: Makatea. Collected by E. Aubert de la
 821 Rüe in 1955.

822 **Diagnosis**: Shell less than 7 mm in diameter, robust, subdepressed,
 823 flammulated; teleoconch sculptured by narrow, very low, relatively crowded
 824 primary axial ribs (>100 ribs on body wall); umbilicus U-shaped; palatal
 825 wall usually with five, rarely with four or six barriers, rarely accompanied by
 826 a trace; parietal wall with three barriers, rarely accompanied by up to three
 827 traces.

828 **Description:** Shell subdepressed, white, with regularly spaced, amber
829 flammulations, usually stronger apically than on body whorl, fading out on
830 the shell base. Shell wall robust, opaque; periostracum adherent, matt.
831 Apex barely elevated, spire moderately raised; whorls descending
832 progressively more rapidly. Whorls and periphery rounded. Apical and
833 umbilical sutures impressed. Transition between protoconch and teleoconch
834 indistinct. Sculpture of the first whorl unknown; second whorl onwards
835 ornamented by a primary sculpture of prominent axial ribs, with interspaces
836 two to four times their width and by a secondary sculpture of fine, crowded
837 axial riblets, with interspaces approximately equal to twice their width;
838 secondary riblets occupying the interspaces between each pair of primary
839 ribs. Spiral cording present from the fourth whorl onwards, overlaying the
840 axial sculpture. Umbilicus very deep, U-shaped, slightly narrower apically
841 than at last whorl. Peristome crescent-shaped; columellar lip slightly
842 reflected. Palatal barriers usually five, rarely four or six in number, slightly
843 recessed within aperture, approximately equidistant; barrier 1 columellar in
844 position, extending beyond the line of vision from the aperture, usually
845 similar to barrier 5 in prominence, occasionally represented by a trace, rarely
846 absent; barriers 2 to 5 extending approximately $1/8$ whorl, with gradual
847 posterior descension; anterior descension of barrier 2 usually sharper than
848 that of barriers 3 to 5; barriers 2 to 4 similar in prominence, taller and wider
849 than barriers 1 and 5; barrier 3 rarely duplicated, raising the number of
850 palatals to six. Palatal trace rarely present, positioned near the apical
851 suture. Parietal wall with three barriers and, rarely, up to three traces;
852 barriers similar in prominence, approximately equidistant, extending slightly
853 less than $3/16$ whorl; trace 1, when present, positioned near the apical
854 suture or between barriers 2 and 3; traces 2 and 3, when present, positioned

855 between barrier 3 and umbilical suture. Other shell features that can be
856 expressed numerically are shown in Table 2.

857 **Remarks:** *K. hypsus* was previously known only from the severely worn
858 holotype (Fig. 20A). Specimens recovered from station Mk19 reveal the
859 coloration pattern of the species (Fig. 20B–C), details of its sculpture and
860 intraspecific variation in the number and arrangement of the apertural
861 barriers (Fig. 21). Fully grown specimens of *K. hypsus* are easily separated
862 from other representatives of the genus by the very large size and robust
863 build of their shells. A comparatively high aperture (width approximately
864 equal to the height) provides the best criterion for identifying specimens
865 with a whorl count of 5 or less (Fig. 20C).

866 [FIGURE 20 approximately here]

867 [FIGURE 21 approximately here]

868 ***Kleokyphus cowiei* sp. nov.**

869 Figures 20D; 22; 35M; 37E; 39.

870

871 **Examined material** (188 specimens). **Holotype:** MNHN 25580, Mk12.

872 **Paratypes:** MNHN 25581, 8 shells, Mk12. **Additional material:** 173
873 shells, Mk12; 6 shells, Mk08.

874 **Type locality:** Approximately 1 km. north of Temao port (15.81638°S;
875 148.27639°W). Large fault in the cliff, shaded. Ferns. Limestone, alt. 10 m.;
876 station Mk12.

877 **Diagnosis:** Shell less than 5 mm in diameter, robust, depressed, usually
878 without markings, seldom flammulated; teleoconch sculptured by broad, low,

879 relatively crowded primary axial ribs (>90 ribs on body wall); umbilicus
880 U-shaped; palatal wall with four barriers and commonly one trace; parietal
881 wall with three barriers.

882 **Description:** Shell depressed, white to fawn, usually without markings,
883 seldom with faint, regularly spaced, amber flammulations. Shell wall
884 moderately robust, opaque; periostracum adherent, shiny. Apex and spire
885 elevated; later whorls descending more rapidly. Apical and umbilical sutures
886 impressed; whorls and periphery rounded; basal and columellar walls
887 transitioning smoothly. Transition between protoconch and teleoconch
888 indistinct. Protoconch sculptured by fine axial riblets, initially with
889 interspaces ten to fifteen times their width, undifferentiated; axial riblets
890 progressively differentiating from the second half of the first whorl onwards,
891 some increasing in prominence and transitioning into the primary ribs of the
892 teleoconch, others becoming close-set and wobbly, transitioning into the
893 secondary riblets of the teleoconch. Spiral sculpture of the protoconch
894 comprising approximately equidistant lirae with interspaces three to five
895 times their width, persisting on the surface of the teleoconch, forming tiny
896 nodules at intersections with the secondary axial sculpture. Primary axial
897 sculpture of the teleoconch comprising broad, prominent ribs, with
898 interspaces approximately equal to twice their width, overlaid by a
899 secondary axial sculpture of fine, crowded, wavy riblets, with interspaces
900 approximately equal to twice their width. Umbilicus deep, U-shaped.
901 Peristome crescent-shaped; columellar lip slightly reflected. Palatal wall with
902 four barriers, all basal in position, extending approximately 1/8 whorl, with
903 gradual anterior and posterior descension, regularly spaced, recessed within
904 the aperture; barriers 1 and 4 more deeply recessed and slightly less
905 prominent than remainder. Deeply recessed palatal trace commonly present,

906 columellar in position. Parietal wall with three barriers, extending
 907 approximately 3/16 whorl, with somewhat abrupt anterior and posterior
 908 descension, regularly spaced, not recessed within the aperture; barrier 1
 909 often slightly less prominent than barrier 2; barrier 2 often slightly less
 910 prominent than barrier 3. Other shell features that can be expressed
 911 numerically are shown in Table 2.

912 **Remarks:** *K. cowiei* shares with *K. hypsus* an U-shaped umbilicus, a
 913 similar arrangement of apertural barriers, and a robust shell, heavier than
 914 those of species of *Mautodontha* (*Garrettoconcha*) Solem, 1976. It is
 915 distinguished from *K. hypsus* by its smaller shell size and lower peristome.
 916 Specimens with a higher spire approach the shell shape of *M. (G.) passosi*,
 917 but are easily distinguished by their larger, heavier shell, and by exhibiting
 918 three rather than two parietal barriers.

919 **Etymology:** This species is dedicated to Robert Cowie, in recognition of
 920 his efforts to understand and preserve the land snail fauna of Pacific islands.

921 [FIGURE 22 approximately here]

922 [Table 2 approximately here]

923 **Genus *Pseudolibera* Solem, 1976**

924 *Pseudolibera* Solem, 1976: 383. Type species (by original designation):

925 *Pseudolibera lillianae* Solem, 1976.

926

927 ***Pseudolibera lillianae* Cooke & Solem, 1976**

928 *Libera* sp. Cooke 1934, pp. 5–6.

929 *Endodonta obolus* (Gould) — Aubert de la Rüe & Soyer 1958, p. 365, *non Helix*
 930 *obolus* Gould 1846b.

931 *Trochonanina obconica* (Pease) [in part] — Aubert de la Rüe & Soyer 1958,
 932 p. 365, non *Helix obconica* Pease 1865.

933 *Pseudolibera lillianae* Cooke & Solem in Solem 1976, pp. 384–385, figs 168a–b.

934 Figures 23; 24; 36A; 37F; 39.

935

936 **Examined material** (1140 specimens). **Holotype:** BPBM 115805,
 937 Tuamotu Islands: Makatea, 1 mile inland at 250 ft. elevation. Collected on a
 938 hillside around roots of a plant by Mrs G.P. Wilder on October 24, 1932..

939 **Additional material:** MNHN, unregistered, 13 shells, one of which gold
 940 coated, det. A. Solem [presumably collected by E. Aubert de la Rüe in 1955
 941 in Makatea; see remarks below]; MNHN 25589, 18 shells, Mk04; 4 shells,
 942 Mk09; 14 shells, Mk10; 361 shells, Mk12; 362 shells, Mk13; 226 shells, Mk16;
 943 133 shells, Mk19; 6 shells, Mk20; 2 shells, Mk25.

944 **Type locality:** Tuamotu Islands: Makatea, 1 mile inland at 250 ft.
 945 elevation. Collected on a hillside around roots of a plant by Mrs G.P. Wilder
 946 on October 24, 1932.

947 **Diagnosis:** *Pseudolibera* with a depressed, flammulated shell; apex and
 948 spire elevated; peripheral keel long and narrow; teleoconch sculptured by
 949 subequal axial and spiral ribs, reduced on shell base; apertural barrier
 950 extending 1/2 to 1 whorl, not bifurcated.

951 **Description:** Shell depressed, dome-shaped, white, with regularly spaced,
 952 amber flammulations, frequently interrupted at the shell periphery and
 953 vicinity of the umbilicus; flammulations on the shell base larger and fewer,
 954 commonly absent on the last half whorl; shell base rarely tinted with an
 955 amber background coloration, in addition to flammulations. Shell wall thin,
 956 opaque to subpellucid; periostracum adherent, shiny. Apex and spire
 957 elevated, later whorls descending slightly more rapidly. Apical suture

958 addressed at apex, progressively deepening in subsequent whorls; umbilical
959 suture addressed. Whorls concave above and below long, narrow peripheral
960 keel, transitioning into broadly convex toward the apical suture and shell
961 base; confluence of basal and columellar walls initially obtusely angled,
962 developing a keel approximately from the fifth whorl onwards. Transition
963 between protoconch and teleoconch indistinct. Primary axial sculpture of
964 the protoconch comprising relatively broad ribs, with interspaces
965 approximately three times their width; four to six secondary axial riblets
966 occupying the interspaces between primary ribs, each approximately one
967 fifth the width of the primary ribs and wavy in morphology. Primary ribs of
968 the protoconch gradually transitioning into narrower and less conspicuous
969 ribs, which comprise the primary axial sculpture of the teleoconch;
970 secondary riblets of the protoconch persisting as the secondary axial
971 sculpture of the teleoconch. Spiral sculpture developing approximately from
972 the beginning of the third whorl onwards, comprising wavy ribs, similar in
973 prominence and spacing to the primary axial ribs of the teleoconch; nodular
974 projections present at intersections between spiral and axial ribs. Sculpture
975 less prominent on shell base than above periphery. Umbilicus rapidly
976 expanding in diameter for approximately the first three whorls, remaining
977 constant in diameter or expanding slightly from approximately the third to
978 the fifth whorl, subsequently constricted by inward growth of the lower
979 columellar wall and lip. Peristome elongated crescent, with rostrate
980 periphery; columellar lip reflected. Palatal wall devoid of barriers. Parietal
981 wall with one barrier, extending $1/2$ to 1 whorl, positioned slightly closer to
982 the apical than umbilical suture, with gradual anterior and posterior
983 descension, rarely flanked by one trace on each side. Parietal traces, when
984 present, extending approximately $1/4$ whorl. Other shell features that can

985 be expressed numerically are shown in Table 3.

986 **Remarks:** Cooke & Solem in Solem (1976) established *P. lillianae* based
987 on only two specimens—the considerably worn holotype (Fig. 23A) and a
988 very small juvenile specimen collected by Aubert de la Rüe & Soyer (1958)
989 and misidentified as *Endodonta obolus*. Solem (1983, pp. 279–280) noted
990 that, during a subsequent visit to the MNHN, he found several additional
991 specimens of this species mixed in a lot which Aubert de la Rüe & Soyer
992 (1958) had reported as “*Trochonanina obconica*”, which also contained three
993 new species of the genus. Solem’s premature death prevented him from
994 establishing those three new species; they are described herein as *P. solemi*
995 sp. nov., *P. aubertdelaruei* sp. nov. and *P. extincta* sp. nov. As for the
996 specimens of *P. lillianae* collected by Aubert de la Rüe & Soyer (1958) and
997 recognized by Solem (1983), it seems clear that they are contained in the
998 first lot we list in our examined material, even though the lot now lacks
999 labels detailing its history and collection data. The lot contained 14
1000 specimens, but one of them proved to be *P. solemi* sp. nov.

1001 *P. lillianae* was the most abundant *Pseudolibera* in the material recovered
1002 in 2005 (Fig. 39). A few well-preserved specimens were found, which reveal
1003 the color pattern of the species (Fig. 23B) and details of its sculpture
1004 (Fig. 24A–C). Only one specimen among the hundreds recovered displayed
1005 parietal traces in addition to the single barrier (Fig. 24D). *P. lillianae* is the
1006 largest *Pseudolibera* in shell diameter and the only species of the genus with
1007 a long and narrow peripheral keel that is frequently chipped off.

1008 [FIGURE 23 approximately here]

1009 [FIGURE 24 approximately here]

1010 *Pseudolibera solemi* sp. nov.

1011 *Trochonanina obconica* (Pease) [in part] — Aubert de la Rüe & Soyler 1958,
1012 p. 365, non *Helix obconica* Pease 1865.

1013 Figures 25A; 26; 36I; 38A; 39.

1014

1015 **Examined material** (114 specimens). **Holotype:** MNHN 25590, Mk16.

1016 **Paratypes:** MNHN 25591, 8 shells, Mk16. **Additional material:**

1017 MNHN, unregistered, 3 shells, one of which gold coated, “*Pseudolibera*
1018 *makateaensis* n.sp.” (undescribed by A. Solem) #1 [*nomen nudum*; collected
1019 by E. Aubert de la Rüe in 1955 in Makatea; see remarks below]; 17 shells,
1020 Mk04; 13 shells, Mk12; 1 shell, Mk13; 10 shells, Mk16; 6 shells, Mk19. 8
1021 shells, Mk21; 47 shells, Mk22.

1022 **Type locality:** Road descending to Temao (15.82593°S; 148.27534°W).

1023 Lower side of the road below rocks. Limestone, alt. 10 m.; station Mk16.

1024 **Diagnosis:** *Pseudolibera* with a depressed to subdepressed, flammulated
1025 shell; apex barely to strongly raised, spire elevated; peripheral keel short and
1026 trigonal; teleoconch sculptured by subequal axial and spiral ribs, very
1027 slightly reduced on shell base; apertural barrier extending 3/4 to 2 whorls,
1028 not bifurcated.

1029 **Description:** Shell depressed to subdepressed, dome-shaped to trigonal,
1030 white, with regularly spaced, amber flammulations on the shell periphery,
1031 tapering apically, usually absent on shell base; commonly with a fawn to
1032 light orange background coloration and a maroon tint on the last whorl.
1033 Shell wall thin, opaque to subpellucid; periostracum adherent, shiny. Apex
1034 barely to strongly raised; spire elevated, latter whorls descending more
1035 rapidly. Apical suture shallowly impressed at apex, progressively deepening
1036 in subsequent whorls; umbilical suture adpressed. Whorls gently concave

1037 above and below relatively short, trigonal peripheral keel, transitioning into
1038 broadly convex toward the apical suture and shell base; confluence of basal
1039 and columellar walls initially obtusely angled, developing a keel
1040 approximately from the fourth whorl onwards. Transition between
1041 protoconch and teleoconch indistinct. Primary axial sculpture of the
1042 protoconch comprising low, narrow ribs, with interspaces two to four times
1043 their width; two to four secondary axial riblets, each approximately half the
1044 width of the primary ribs and wavy in morphology, occupying the
1045 interspaces between primary ribs. Primary ribs of the protoconch gradually
1046 transitioning into broader and taller ribs, which comprise the primary axial
1047 sculpture of the teleoconch; secondary riblets of the protoconch gradually
1048 increasing in number and persisting as the secondary axial sculpture of the
1049 teleoconch. Spiral sculpture developing approximately from the third whorl
1050 onwards, comprising wavy ribs, more closely spaced and slightly lower than
1051 the primary axial ribs of the teleoconch; nodular projections present at
1052 intersections between spiral and axial ribs. Axial sculpture very slightly
1053 reduced on shell base. Umbilicus rapidly expanding in diameter for
1054 approximately the first three whorls, remaining constant in diameter for
1055 approximately one whorl, subsequently constricted by inward growth of the
1056 lower columellar wall and lip. Peristome elongated crescent, with rostrate
1057 periphery; columellar lip reflected. Palatal wall devoid of barriers. Parietal
1058 wall with one barrier, positioned slightly closer to the apical than umbilical
1059 suture, with gradual anterior and posterior descension, varying in length
1060 from approximately 3/4 to 2 whorls. Other shell features that can be
1061 expressed numerically are shown in Table 3.

1062 **Remarks:** A lot labelled as “*Pseudolibera makateaensis* n.sp.
1063 (undescribed by A. Solem) #1” in the collections of the MNHN indicates

1064 that *P. solemi* is one of three undescribed species Solem recognized among
1065 the material Aubert de la Rüe & Soyer (1958) had erroneously reported as
1066 *Trochonanina obconica*. The lot contained two specimens, one of which gold
1067 coated; to these we added one shell with the same presumed origin that
1068 Solem had misidentified as *P. lilliana*. Solem (1983, p. 280) cited his study
1069 of the three undescribed species as “in preparation”, but a search for his
1070 unpublished manuscript in the archives of the FMNH proved unfruitful (J.
1071 Gerber, personal communication 2012). Analysis of these specimens and
1072 numerous matching shells collected in 2005 revealed that they indeed
1073 represent a new species.

1074 *P. solemi* displays considerable variation in the prominence and length of
1075 its apertural barrier. In at least two of the specimens studied by Solem and
1076 in six from the type locality (station Mk16) the barrier extends posteriorly
1077 for more than 1 whorl from the peristome and, at its highest point, reaches
1078 approximately half the height of the aperture. The barrier was found to
1079 extend for approximately 2 whorls in one of these individuals (Fig. 26D), but
1080 1.5 whorl seems more typical. In specimens collected elsewhere, the
1081 apertural barrier appears to reach only half the height recorded at Mk16,
1082 and to vary between 0.75 and 1 whorl in extension, with the latter
1083 configuration more frequent. *P. solemi* is also somewhat variable in the
1084 elevation of its apex and spire. Specimens with a lower spire approach the
1085 shape of *P. lilliana*, but they may be distinguished from that species by a
1086 smaller shell size at the same number of whorls, shorter and more trigonal
1087 peripheral keel, flammulations more spaced and restricted to the shell
1088 periphery, and by more prominent sculpture on the shell base. With further
1089 study and additional material, *P. solemi* may prove to be a complex of
1090 similar species differing only in details of shell shape and morphology of the

1091 apertural barrier. At present regional differences seem too small and
 1092 complex to warrant formal recognition.

1093 **Etymology:** This species is dedicated to Alan Solem, who first
 1094 recognized this species and whose monographs on endodontids have provided
 1095 the foundation for all subsequent studies of the family.

1096 [FIGURE 25 approximately here]

1097 [FIGURE 26 approximately here]

1098 *Pseudolibera matthiewi* sp. nov.

1099 Figures 25B; 27; 36D; 38E; 39.

1100

1101 **Examined material** (118 specimens). **Holotype:** MNHN 26531, Mk13.

1102 **Paratypes:** MNHN 26532, 8 shells, Mk13. **Additional material:** 1 shell,
 1103 Mk03; 2 shells, Mk04; 101 shells, Mk13; 1 shell, Mk16; 1 shell, Mk19; 3 shell,
 1104 Mk22.

1105 **Type locality:** West coast, approximately 3 km south of Temao
 1106 (15.85189°S; 148.28018°W). Cave. Limestone, alt. 10 m.; station Mk13.

1107 **Diagnosis:** *Pseudolibera* with a depressed, flammulated shell; apex
 1108 depressed to barely raised, spire elevated; peripheral keel narrow; teleoconch
 1109 sculptured by subequal axial and spiral ribs, not reduced on shell base;
 1110 apertural barrier extending $1\frac{1}{2}$ whorl, with a bifurcated mid sector.

1111 **Description:** Shell depressed, dome-shaped, white, with regularly spaced,
 1112 amber flammulations on the apical surface, absent or restricted to the
 1113 peripheral keel on the shell base. Shell wall very thin, opaque to pellucid;

1114 periostracum adherent, shiny. Apex depressed to barely raised; spire
1115 elevated, latter whorls descending more rapidly. Apical suture impressed at
1116 apex, progressively deepening in subsequent whorls; umbilical suture
1117 impressed at apex, adpressed approximately from the third whorl onwards.
1118 Whorls concave above and below narrow peripheral keel, transitioning into
1119 broadly convex toward the apical suture and shell base; confluence of basal
1120 and columellar walls initially obtusely angled, developing a keel
1121 approximately from the sixth whorl onwards. Transition between protoconch
1122 and teleoconch indistinct. Protoconch sculptured by relatively broad
1123 primary axial ribs, with interspaces two to three times their width, overlaid
1124 by a fine secondary sculpture of oblique, axial and spiral elements; oblique
1125 elements represented by irregular riblets on the first whorl, gradually
1126 transitioning into axial riblets with interspaces approximately equal to their
1127 width; secondary spiral sculpture of the protoconch comprising fine lirae,
1128 with interspaces approximately four times their width, forming tiny nodules
1129 at intersections with oblique and axial riblets. Primary ribs of the
1130 protoconch gradually transitioning into taller ribs, which comprise the
1131 primary axial sculpture of the teleoconch; secondary axial riblets of the
1132 protoconch gradually increasing in number and persisting as the secondary
1133 axial sculpture of the teleoconch. Spiral sculpture of the protoconch
1134 transitioning into wavy spiral ribs of the teleoconch, more closely spaced and
1135 slightly lower than the primary axial ribs of the teleoconch; nodular
1136 projections present at intersections between spiral and axial ribs. Sculpture
1137 not reduced on shell base. Umbilicus rapidly expanding in diameter for
1138 approximately the first three whorls, remaining constant in diameter for
1139 approximately two whorls, subsequently constricted by inward growth of the
1140 lower columellar wall and lip. Peristome elongated crescent, with rostrate

1141 periphery; columellar lip reflected. Palatal wall devoid of barriers. Parietal
 1142 wall with one barrier, positioned slightly closer to the apical than umbilical
 1143 suture, with gradual anterior and posterior descension, extending posteriorly
 1144 for approximately $1\frac{1}{2}$ whorl, with a bifurcated tip along its mid sector; onset
 1145 of bifurcated tip approximately $1/2$ to $3/4$ whorl behind the aperture; offset
 1146 of bifurcated tip approximately $1\frac{1}{4}$ whorl behind the aperture. Other shell
 1147 features that can be expressed numerically are shown in Table 3.

1148 **Remarks:** The bifurcated sector of its parietal barrier distinguishes
 1149 *P. matthieui* from all other *Pseudolibera*. However, the Y-shaped sector of
 1150 the barrier lies deeply within the aperture and is not observable in intact
 1151 specimens using reflected or transmitted light. The flatter apex of
 1152 *P. matthieui* provides the best feature for distinguishing intact specimens
 1153 from the somewhat similar *P. lilliana*e, *P. solemi* and *Pseudolibera cookei*
 1154 sp. nov. Additionally, *P. matthieui* differs from *P. lilliana*e in its deeper
 1155 sutures, smaller body size and slightly shorter peripheral keel; from
 1156 *P. solemi* in its narrower peripheral keel, more frequent and larger
 1157 flammulations, and in its usually lower spire; and from *Pseudolibera cookei*
 1158 in its deeper sutures, more crowded and less conspicuous axial sculpture,
 1159 and in exhibiting spiral sculpture on the shell base.

1160 Examining damaged or carefully excised shells of *P. matthieui*, we verified
 1161 the morphology of the barrier in one shell each from stations Mk04, Mk16,
 1162 Mk19 and Mk22, and in twenty-three individuals from the type locality
 1163 (Mk13). All specimens from the west coast of Makatea (stations Mk13 and
 1164 Mk16) have the first two whorls flat to barely raised, whereas individuals
 1165 from the east coast (stations Mk03, Mk04, Mk19 and Mk22) exhibit a
 1166 depressed spire for the first four whorls (Fig. 27E). Unfortunately, only a few
 1167 specimens were found on the east coast and all but one are not fully grown,

1168 making the significance of the difference in initial growth difficult to assess.
1169 Differences in coloration and sculpture between individuals from the west
1170 and east coast appear to be minor.

1171 **Etymology:** This species is dedicated to Matthieu Fontaine, son of the
1172 third author.

1173 [FIGURE 27 approximately here]

1174 *Pseudolibera cookei* sp. nov.

1175 Figures 25C; 28; 36G; 38D; 39.

1176

1177 **Examined material** (9 specimens). **Holotype:** MNHN 25675, Mk13.

1178 **Paratypes:** MNHN 25676, 8 shells, Mk13.

1179 **Type locality:** West coast, approximately 3 km south of Temao
1180 (15.85189°S; 148.28018°W). Cave. Limestone, alt. 10 m.; station Mk13.

1181 **Diagnosis:** *Pseudolibera* with a depressed, tinted shell; apex and spire
1182 elevated; peripheral keel slightly angled towards the shell base; teleoconch
1183 sculptured by coarse, relatively well-spaced primary axial ribs (<100 ribs on
1184 body whorl) and low spiral riblets, the former much reduced and the latter
1185 absent on shell base; apertural barrier extending 3/4 whorl, not bifurcated.

1186 **Description:** Shell depressed, dome-shaped, white, with an amber tint
1187 covering most of the surface, absent from the vicinity of the umbilicus. Shell
1188 wall thin, opaque to subpellucid; periostracum adherent, shiny. Apex and
1189 spire elevated, latter whorls descending slightly more rapidly. Apical suture
1190 adpressed at apex, progressively deepening in subsequent whorls; umbilical
1191 suture impressed at apex, adpressed approximately from the third whorl
1192 onwards. Peripheral keel slightly angled towards the shell base; whorls

1193 concave above and below peripheral keel, transitioning into broadly convex
1194 toward the apical suture and shell base; confluence of basal and columellar
1195 walls initially obtusely angled, developing a keel approximately from the
1196 fourth whorl onwards. Transition between protoconch and teleoconch
1197 indistinct. Primary axial sculpture of the protoconch comprising relatively
1198 broad ribs, with interspaces approximately three times their width; four to
1199 six secondary axial riblets, each approximately one fifth the width of the
1200 primary ribs and wavy in morphology, occupying the interspaces between
1201 primary ribs. Primary ribs of the protoconch gradually transitioning into
1202 taller ribs, which comprise the primary axial sculpture of the teleoconch;
1203 secondary riblets of the protoconch gradually increasing in number and
1204 persisting as the secondary axial sculpture of the teleoconch. Spiral
1205 sculpture developing approximately from the third whorl onwards,
1206 comprising very low, broad riblets, with interspaces similar to their width,
1207 forming nodules at intersections with the axial sculpture. Spiral sculpture
1208 absent and axial sculpture much reduced on shell base. Umbilicus rapidly
1209 expanding in diameter for approximately the first three whorls, remaining
1210 constant in diameter for approximately one whorl, subsequently constricted
1211 by inward growth of the lower columellar wall and lip. Peristome elongated
1212 crescent, with rostrate periphery; columellar lip reflected. Palatal wall
1213 devoid of barriers. Parietal wall with one barrier, extending approximately
1214 $3/4$ whorl, positioned slightly closer to the apical than umbilical suture, with
1215 gradual anterior and posterior descension. Other shell features that can be
1216 expressed numerically are shown in Table 3.

1217 **Remarks:** The prominent and well-spaced axial sculpture of *P. cookei*
1218 confers a pleated aspect to its shell periphery and, together with the absence
1219 of spiral sculpture on the shell base, comprise the best features to

1220 distinguish this species from similarly shaped *Pseudolibera*, namely
 1221 *P. lillianae*, *P. solemi* and *P. matthiewi*.

1222 **Etymology:** This species is dedicated to Charles Montague Cooke, Jr.,
 1223 pioneer of the study of the malacofauna of Makatea.

1224 [FIGURE 28 approximately here]

1225 ***Pseudolibera aubertdelaruei* sp. nov.**

1226 *Trochonanina obconica* (Pease) [in part] — Aubert de la Rüe & Soyer 1958,
 1227 p. 365, non *Helix obconica* Pease 1865.

1228 Figures 25D; 29; 36E.

1229

1230 **Examined material** (3 specimens). **Holotype:** MNHN 25673,
 1231 “*Pseudolibera spiralis* n.sp.” (undescribed by A. Solem) #3 [*nomen nudum*;
 1232 collected by E. Aubert de la Rüe in 1955 in Makatea; see remarks below].

1233 **Paratypes:** MNHN 25674, 2 shells, one of which gold coated, “*Pseudolibera*
 1234 *spiralis* n.sp.” (undescribed by A. Solem) #3 [*nomen nudum*; collected by E.
 1235 Aubert de la Rüe in 1955 in Makatea; see remarks below].

1236 **Type locality:** Tuamotu Islands: Makatea.

1237 **Diagnosis:** *Pseudolibera* with a depressed, flammulated shell; apex flat,
 1238 spire elevated; peripheral keel very short, trigonal; teleoconch sculptured by
 1239 very low axial and spiral riblets, not reduced on shell base; apertural barrier
 1240 extending $1\frac{1}{8}$ whorl, not bifurcated.

1241 **Description:** Shell depressed, dome-shaped, white, with regularly spaced,
 1242 amber flammulations on the apical surface, absent on the shell base. Shell
 1243 wall very thin, subpellucid to pellucid; periostracum adherent, shiny. Apex
 1244 flat; spire elevated; whorls descending progressively more rapidly. Apical

1245 suture adpressed; umbilical suture shallowly impressed. Whorls sharply
1246 concave above and gently concave below very short, trigonal peripheral keel,
1247 transitioning into broadly convex toward the apical suture and shell base;
1248 confluence of basal and columellar walls initially obtusely angled, developing
1249 a keel approximately from the fifth whorl onwards. Transition between
1250 protoconch and teleoconch indistinct. Protoconch sculptured by fine, low
1251 axial riblets, with interspaces approximately equal to three times their
1252 width, gradually transitioning into slightly broader and taller riblets, which
1253 comprise the primary axial sculpture of the teleoconch. Secondary axial
1254 sculpture of the teleoconch comprising fine lirae. Spiral sculpture developing
1255 approximately from the last quarter of the third whorl onwards, comprising
1256 riblets similar in morphology and spacing to the primary axial riblets,
1257 forming tiny nodules at intersections with the axial elements of sculpture.
1258 Sculpture not reduced on shell base. Umbilicus rapidly expanding in
1259 diameter for approximately the first three whorls, remaining constant in
1260 diameter for approximately two whorls, subsequently constricted by inward
1261 growth of the lower columellar wall and lip. Peristome subquadrate;
1262 columellar lip reflected. Palatal wall devoid of barriers. Parietal wall with
1263 one barrier, positioned slightly closer to the apical than umbilical suture,
1264 with gradual anterior and posterior descension, extending for approximately
1265 $1\frac{1}{8}$ whorl. Other shell features that can be expressed numerically are shown
1266 in Table 3.

1267 **Remarks:** *P. aubertdelaruei* is one of three undescribed species Solem
1268 recognized among the material Aubert de la Rüe & Soyer (1958) had
1269 erroneously reported as *Trochonanina obconica* (see remarks under *P. solemi*
1270 for details). Our efforts to locate additional specimens have failed and the
1271 species is thus established based solely on the three specimens collected by

1272 Aubert de la Rüe in Makatea, without more precise geographic data. The
 1273 holotype is the largest specimen and paratype 1 is the shell coated in gold,
 1274 presumably by Solem. The much reduced axial sculpture of
 1275 *P. aubertdelaruei*, which is too feeble to count (Table 3), immediately sets it
 1276 apart from other *Pseudolibera*.

1277 **Etymology:** This species is dedicated to Edgar Aubert de la Rüe, who
 1278 collected the only known specimens of this taxon.

1279 [FIGURE 29 approximately here]

1280 ***Pseudolibera extincta* sp. nov.**

1281 *Trochonanina obconica* (Pease) [in part] — Aubert de la Rüe & Soyer 1958,
 1282 p. 365, non *Helix obconica* Pease 1865.

1283 Figures 30A; 31; 36F; 38C; 39.

1284

1285 **Examined material** (30 specimens). **Holotype:** MNHN 25592, Mk16.

1286 **Paratypes:** MNHN 25593, 8 shells, Mk16 **Additional material:** MNHN,
 1287 unregistered, 3 shells, one of which gold coated, “*Pseudolibera depressa*
 1288 n.sp.” (undescribed by A. Solem) #4 [*nomen nudum*; collected by E. Aubert
 1289 de la Rüe in 1955 in Makatea; see remarks below]; 15 shell, Mk16; 3 shells,
 1290 Mk12.

1291 **Type locality:** Road descending to Temao (15.82593°S; 148.27534°W).

1292 Lower side of the road below rocks. Limestone, alt. 10 m.; station Mk16.

1293 **Diagnosis:** *Pseudolibera* with a depressed, flammulated shell; apex
 1294 depressed, spire elevated; peripheral keel upturned; teleoconch sculptured by
 1295 crowded axial ribs (>150 ribs on body whorl) and spiral lirae, not reduced
 1296 on shell base; apertural barrier extending $1\frac{1}{2}$ whorl, not bifurcated.

1297 **Description:** Shell depressed, dome-shaped, white, with regularly spaced,
1298 amber flammulations on the apical surface, absent on the shell base. Shell
1299 wall thin, opaque to subpellucid; periostracum adherent, shiny. Apex and
1300 first $2\frac{1}{2}$ whorls depressed; spire elevated; later whorls descending
1301 progressively more rapidly. Apical suture shallowly impressed at apex,
1302 gradually transitioning to adpressed by the end of the third whorl,
1303 progressively deepening from the fourth whorl onwards; umbilical suture
1304 impressed at apex, adpressed approximately from the fourth whorl onwards.
1305 Whorls sharply concave immediately above upturned peripheral keel,
1306 forming a well-defined groove between keel and supraproperipheral wall; broadly
1307 convex from the apical suture to the vicinity of the groove. Shell base
1308 broadly convex, transitioning into gently concave in the vicinity of the
1309 peripheral keel; confluence of basal and columellar walls initially obtusely
1310 angled, developing a keel approximately from the fifth whorl onwards.
1311 Transition between protoconch and teleoconch indistinct. Protoconch
1312 sculpture by fine axial riblets, with interspaces approximately two to three
1313 times their width, and by minute spiral lirae, with interspaces approximately
1314 equal to three times their width. Axial riblets of the protoconch gradually
1315 transitioning into broader and taller ribs, which comprise the primary axial
1316 sculpture of the teleoconch. Secondary axial sculpture of the teleoconch
1317 comprising minute lirae, with interspaces approximately equal to their width.
1318 Spiral lirae of the protoconch persisting on the surface of the teleoconch,
1319 forming tiny nodules at intersections with axial lirae. Sculpture not reduced
1320 on shell base. Umbilicus rapidly expanding in diameter for approximately
1321 the first three whorls, remaining constant in diameter for approximately two
1322 whorls, subsequently constricted by inward growth of the lower columellar
1323 wall and lip. Peristome subquadrate; columellar lip reflected. Palatal wall

1324 devoid of barriers. Parietal wall with one barrier, positioned slightly closer
1325 to the apical than umbilical suture, with gradual anterior and posterior
1326 descension, extending for approximately $1\frac{1}{2}$ whorl. Other shell features that
1327 can be expressed numerically are shown in Table 3.

1328 **Remarks:** *P. extincta* is one of three undescribed species Solem
1329 recognized among the material Aubert de la Rüe & Soyer (1958) had
1330 erroneously reported as *Trochonanina obconica* (see remarks under *P. solemi*
1331 for details). It is easily distinguished from other *Pseudolibera* by its
1332 depressed apex, upturned peripheral keel, and by its teleoconch sculpture of
1333 crowded, low axial ribs and much reduced spiral lirae.

1334 **Etymology:** From the latin *extinctio*, in reference to the fate of much of
1335 the native endodontid fauna of Pacific islands.

1336 [FIGURE 30 approximately here]

1337 [FIGURE 31 approximately here]

1338 ***Pseudolibera paraminderæ* sp. nov.**

1339 Figures 30B; 32; 36C; 38C; 39.

1340

1341 **Examined material** (123 specimens). **Holotype:** MNHN 25677, Mk04.

1342 **Paratypes:** MNHN 25678, 8 shells, Mk04. **Additional material:** 61
1343 shells, Mk04; 19 shells, Mk09; 34 shells, Mk10.

1344 **Type locality:** Moumu cave (15.83347°S; 148.24933°W). Deposits inside
1345 cave. Limestone, alt. 30 m.; station Mk04.

1346 **Diagnosis:** *Pseudolibera* with a depressed, flammulated shell; apex and
1347 spire elevated; peripheral keel upturned from the fifth whorl onwards;

1348 teleoconch sculptured by crowded axial ribs (>150 ribs on body whorl) and
1349 spiral riblets, the latter present only on the shell base; apertural barrier
1350 extending 1/2 whorl, not bifurcated.

1351 **Description:** Shell depressed, dome-shaped, white to light fawn, with
1352 regularly spaced, amber flammulations on the apical surface, absent on the
1353 shell base; flammulations fading out on the sixth whorl. Shell wall thin,
1354 opaque to subpellucid; periostracum adherent, shiny. Apex and spire
1355 elevated; later whorls descending slightly more rapidly. Apical suture
1356 adpressed at apex, progressively deepening in subsequent whorls; umbilical
1357 suture adpressed. Initial four whorls gently concave above peripheral keel,
1358 transitioning from the fifth whorl onwards into sharply concave, with an
1359 upturned peripheral keel and conspicuous supraperipheral groove. Whorls
1360 broadly convex in the vicinity of the apical suture and on shell base; gently
1361 concave below the peripheral keel; confluence of basal and columellar walls
1362 initially obtusely angled, developing a keel approximately from the fifth
1363 whorl onwards. Transition between protoconch and teleoconch indistinct.
1364 Primary axial sculpture of the protoconch comprising relatively broad ribs,
1365 with interspaces approximately twice to three times their width; two to four
1366 secondary axial riblets, each approximately one fifth the width of the
1367 primary ribs and wavy in morphology, occupying the interspaces between
1368 primary ribs. Primary ribs of the protoconch gradually transitioning into
1369 narrower ribs, slightly taller peripherally than above and below peripheral
1370 keel, which comprise the primary axial sculpture of the teleoconch; secondary
1371 riblets of the protoconch gradually increasing in number and persisting as
1372 the secondary axial sculpture of the teleoconch. Axial sculpture not reduced
1373 on shell base. Spiral sculpture present only on the shell base, restricted to
1374 the vicinity of the umbilicus or frequently extending almost to the peripheral

1375 keel, comprising riblets with interspaces approximately equal to twice their
1376 width; spiral riblets forming nodular projections at intersections with axial
1377 ribs and riblets. Umbilicus rapidly expanding in diameter for approximately
1378 the first three whorls, remaining constant in diameter for approximately one
1379 whorl, subsequently constricted by inward growth of the lower columellar
1380 wall and lip. Peristome subquadrate; columellar lip reflected. Palatal wall
1381 devoid of barriers. Parietal wall with one barrier, positioned slightly closer
1382 to the apical than umbilical suture, with gradual anterior and posterior
1383 descension, extending for approximately 1/2 whorl. Other shell features that
1384 can be expressed numerically are shown in Table 3.

1385 **Remarks:** A marked change in the concavity of the suprapерipheral wall,
1386 with the peripheral keel upturned from the fifth whorl onwards, is a unique
1387 feature of *P. paraminderae*, and the easiest criterion for recognizing
1388 fully-grown specimens. Specimens displaying less than five whorls are very
1389 similar to *P. lillianae* in general shell shape, but are easily distinguished
1390 from that species by their lack of spiral sculpture on the apical surface, as
1391 well as by their smaller shell size.

1392 **Etymology:** This species is dedicated to Paraminder Dhillon, wife of the
1393 first author.

1394 [FIGURE 32 approximately here]

1395 ***Pseudolibera elieporoi* sp. nov.**

1396 Figures 30C; 33 36H; 38D; 39.

1397

1398 **Examined material** (93 specimens). **Holotype:** MNHN 25594, Mk04.

1399 **Paratypes:** MNHN 25595, 8 shells, Mk04. **Additional material:** 65

1400 shells, Mk04; 9 shells, Mk09; 10 shells, Mk10.

1401 **Type locality:** Moumu cave (15.83347°S; 148.24933°W). Deposits inside
1402 cave. Limestone, alt. 30 m.; station Mk04.

1403 **Diagnosis:** *Pseudolibera* with a subdepressed, flammulated shell; apex
1404 and spire elevated; peripheral keel short, trigonal; teleoconch sculptured by
1405 subequal axial and spiral ribs, not reduced on the shell base; apertural
1406 barrier extending $1\frac{1}{8}$ whorl, not bifurcated.

1407 **Description:** Shell subdepressed, dome-shaped, white, with regularly
1408 spaced, amber flammulations, often more conspicuous on shell base than
1409 apically. Shell wall thin to moderately robust, subpellucid to opaque;
1410 periostracum adherent, shiny. Apex and spire elevated; later whorls
1411 descending more rapidly. Apical suture adpressed; umbilical suture
1412 impressed at apex, adpressed approximately from the third whorl onwards.
1413 Whorls gently concave above and below short, trigonal peripheral keel,
1414 transitioning into broadly convex toward the apical suture and shell base;
1415 confluence of basal and columellar walls initially obtusely angled, developing
1416 a keel approximately from the fifth whorl onwards. Transition between
1417 protoconch and teleoconch indistinct. Protoconch sculptured by primary
1418 axial ribs, with interspaces three to four times their width, overlaid by a fine
1419 secondary sculpture of oblique, axial and spiral elements; oblique elements
1420 represented by irregular riblets on the first whorl, gradually transitioning
1421 into axial riblets with interspaces approximately equal to their width; spiral
1422 sculpture of the protoconch comprising fine lirae, with interspaces
1423 approximately two to three times their width, forming tiny nodules at
1424 intersections with oblique and axial riblets. Primary ribs of the protoconch
1425 gradually transitioning into taller ribs, which comprise the primary axial
1426 sculpture of the teleoconch; secondary axial riblets of the protoconch

1427 gradually increasing in number and persisting as the secondary axial
 1428 sculpture of the teleoconch. Spiral lirae persisting as the secondary spiral
 1429 sculpture of the teleoconch. Primary spiral sculpture of the teleoconch
 1430 developing from the third whorl onwards, comprising wavy ribs with
 1431 interspaces two to five times their width, slightly less prominent than the
 1432 axial ribs; nodular projections present at intersections between spiral and
 1433 axial elements of sculpture. Sculpture not reduced on shell base. Umbilicus
 1434 rapidly expanding in diameter for approximately the first three whorls,
 1435 remaining constant in diameter for approximately one whorl, subsequently
 1436 constricted by inward growth of the lower columellar wall and lip. Peristome
 1437 subquadrate; columellar lip reflected. Palatal wall devoid of barriers.
 1438 Parietal wall with one barrier, positioned slightly closer to the apical than
 1439 umbilical suture, with gradual anterior and posterior descension, extending
 1440 for approximately $1\frac{1}{8}$ whorl. Other shell features that can be expressed
 1441 numerically are shown in Table 3.

1442 **Remarks:** The comparatively high shell of *P. elieporoi*, with the apical
 1443 suture adpressed throughout ontogeny, differentiates this species from all
 1444 other *Pseudolibera*. Subadults of *P. elieporoi* approach the shell shape of
 1445 *P. aubertdelaruei* (Fig. 33) but are easily distinguished from that species by
 1446 their more prominent sculpture.

1447 **Etymology:** This species is dedicated to Elie Poroi, in recognition of his
 1448 continuous effort to preserve the fenua (Polynesian word for motherland)
 1449 and for welcoming us into Polynesian traditional culture.

1450 [FIGURE 33 approximately here]

1451 *Pseudolibera parva* sp. nov.

1452 Figures 30D; 34; 36B; 37C; 39.

1453

1454 **Examined material** (44 specimens). **Holotype:** MNHN 25679, Mk03.

1455 **Paratypes:** MNHN 25680, 8 shells, Mk03. **Additional material:** 20

1456 shells, Mk03; 4 shells, Mk10; 11 shells, Mk12.

1457 **Type locality:** Road to Moumu, descending between cliffs (15.83496°S;

1458 148.24928°W). Foot of the cliff. Limestone, alt. 50 m.; station Mk03.

1459 **Diagnosis:** *Pseudolibera* with a depressed, flammulated shell, less than 5

1460 mm in diameter; apex flat to slightly raised, spire elevated; peripheral keel

1461 poorly marked; teleoconch sculptured by relatively well-spaced axial ribs

1462 (<100 ribs on body whorl) and by spiral ribs, the former taller than the

1463 latter and reduced in height in the vicinity of the umbilicus; apertural

1464 barrier extending 3/4 whorl, not bifurcated.

1465 **Description:** Shell depressed, white, with regularly spaced, amber to

1466 maroon flammulations, quickly fading out on shell base; first two to three

1467 whorls often with a fawn background coloration, in addition to the

1468 flammulations. Shell wall thin, opaque to subpellucid; periostracum

1469 adherent, shiny. Apex flat to slightly raised; spire elevated; later whorls

1470 descending more rapidly. Apical suture impressed; umbilical suture

1471 adpressed. Whorls very gently concave above and straight below poorly

1472 marked peripheral keel, gradually transitioning into sharply convex toward

1473 the apical suture and gently convex toward the shell base; confluence of

1474 basal and columellar walls initially obtusely angled, developing a keel

1475 approximately from the fourth whorl onwards. Transition between

1476 protoconch and teleoconch indistinct. Protoconch sculptured by primary

1477 axial ribs, with interspaces approximately twice their width, overlaid by a

1478 fine secondary sculpture of oblique, axial and spiral elements; oblique

1479 elements represented by irregular riblets on the first half whorl, gradually
1480 transitioning into axial riblets with interspaces approximately equal to twice
1481 their width; spiral sculpture of the protoconch comprising fine lirae, with
1482 interspaces two to four times their width, forming tiny nodules at
1483 intersections with oblique and axial riblets. Primary ribs of the protoconch
1484 gradually transitioning into taller ribs, which comprise the primary axial
1485 sculpture of the teleoconch; secondary axial riblets of the protoconch
1486 gradually increasing in number and persisting as the secondary axial
1487 sculpture of the teleoconch. Spiral lirae fading out on second whorl, replaced
1488 from the third whorl onwards by the spiral sculpture of the teleoconch.
1489 Spiral ribs of the teleoconch separated by interspaces three to five times
1490 their width, forming nodules at intersections with axial ribs and riblets.
1491 Primary axial ribs of the teleoconch reduced in height in the vicinity of the
1492 umbilicus. Umbilicus rapidly expanding in diameter for approximately the
1493 first three whorls, subsequently constricted by inward growth of the lower
1494 columellar wall and lip. Peristome subquadrate; columellar lip reflected.
1495 Palatal wall devoid of barriers. Parietal wall with one barrier, positioned
1496 slightly closer to the apical than umbilical suture, with gradual anterior and
1497 posterior descension, extending for approximately 3/4 whorl. Other shell
1498 features that can be expressed numerically are shown in Table 3.

1499 **Remarks:** *P parva* is the smallest known species of *Pseudolibera*.
1500 Specimens collected at station Mk12 have the shell more tightly coiled, with
1501 somewhat shallower sutures (Fig. 34D), but in all other aspects are identical
1502 to material from the type locality and vicinity.

1503 **Etymology:** From *parvus* (latin), meaning small, pertaining to the shell
1504 size of this species.

1505 [FIGURE 34 approximately here]

[Table 3 approximately here]

1507 Discussion

1508 The indigenous land snail fauna of Pacific Islands is characterized by high
1509 levels of species richness and endemism (Lydeard *et al.* 2004). Yet, this
1510 fauna is also severely understudied, taxonomic surveys being few and far
1511 apart. In the case of Makatea, the last comprehensive compilation of the
1512 terrestrial malacofauna is that of Cooke (1934), which lists twenty-two
1513 species, including two endodontids. Solem (1976) established two species of
1514 *Kleokyphus* based on material collected in 1955, bringing the total number of
1515 land snail species previously described from the atoll to twenty-four, of
1516 which four are endodontids. Hence, our description of eighteen new species
1517 of the family represents a greater than five-fold increase in the number of
1518 endodontids recognized from Makatea, and brings the total number of land
1519 snails recorded from the island to forty-two species. Although preliminary
1520 analysis of the recently collected samples suggests endodontids are indeed
1521 the most speciose group (personal observations), a fully updated list of the
1522 Makatean malacofauna awaits systematic revision of the other families
1523 involved.

1524 In species richness, the endodontid fauna of Makatea matches that of
1525 Mangareva in the Gambier Islands, with twenty-two species each (Abdou &
1526 Bouchet 2000). These islands are second only to the Austral Island of Rapa
1527 Iti, from where Solem (1976, 1983) reported twenty-four endodontids
1528 (Table 4).

1529 [Table 4 approximately here]

1530 [FIGURE 35 approximately here]

1531 [FIGURE 36 approximately here]

1532 Despite the paucity of data on the malacofauna of the atolls neighboring
1533 Makatea, all of them are saline environments, **sparsely vegetated**, low in
1534 elevation, with a central lagoon (Dupon 1993). As a general rule, they do
1535 not provide suitable habitats for endodontids, which are typically ground
1536 dwellers in dense forests (Solem 1976). The only known exceptions are the
1537 Tuamotu atolls of Anaa and Niau (Fig. 1), from where Solem (1976)
1538 reported specimens of *M. (M.) daedalea*. The nearest sizable islands
1539 sustaining a forest cover are the volcanic Tahiti and Moorea in the Society
1540 Islands, the former located 245 kilometers southwest of Makatea
1541 (Montaggioni *et al.* 1985). Their malacofauna, as that of the Society Islands
1542 in general, is **relatively** well-known **compared to many other** Polynesian
1543 **islands** (Garrett 1884; Gregory 1935; Solem 1976). Therefore, it seems likely
1544 that, except for *M. (M.) daedalea*, all endodontids studied in this paper are
1545 endemic to Makatea. This high level of endemism contrasts with the small
1546 number of endemics identified in the remainder of the Makatean
1547 malacofauna; among twenty species belonging to other land snail families,
1548 Cooke (1934) interpreted only three as possibly restricted to the island.

1549 Within Makatea, a few of the studied endodontids were found to be
1550 widespread (e.g. *M. (M.) daedalea*, *P. lillianae* and *P. solemi*), but most
1551 were restricted to one or a few sampled stations (Figs 37, 38). Several of the
1552 taxa were found in relative abundance at single sites (Fig. 39). *Mautodontha*
1553 (*Mautodontha*) *virginiae*, *M. (G.) aurora*, *M. (G.) passosi*, *M. (G.) spelunca*,
1554 *K. hypsus*, *K. cowiei* and *Pseudolibera matthiewi* were each represented by
1555 more than one hundred specimens in one of the surveyed stations, and by
1556 few shells elsewhere.

1557 The seemingly confined geographic distributions of most of the Makatean
1558 endodontids suggests that further exploration of the malacofauna of

1559 Makatea, particularly in the **less accessible** south, is likely to reveal the
1560 existence of additional new species.

1561 [FIGURE 37 approximately here]

1562 [FIGURE 38 approximately here]

1563 [FIGURE 39 approximately here]

1564 **Relationships**

1565 Two of the three endodontid genera represented in Makatea, *Kleokyphus* and
1566 *Pseudolibera*, are endemic to the island. *Mautodontha*, on the other hand, is
1567 widespread, with representatives in the Tuamotu Archipelago and in the
1568 Austral, Cook and Society Islands (Solem 1983).

1569 *Pseudolibera* is similar to *Libera* Garrett, 1881 and *Gambiodonta* Solem,
1570 1976 in the development of a columellar keel that constricts the umbilicus,
1571 and it resembles *Nesodiscus* Thiele, 1931 in having only one parietal barrier
1572 of great length (Solem 1976). However, species of *Pseudolibera* are unique in
1573 displaying both of these features in conjunction, as well as in their complete
1574 lack of palatal barriers. There is little doubt, therefore, that the genus
1575 represents a monophyletic, *in situ* radiation.

1576 The status of *Kleokyphus* is less clear. Solem (1976, p. 224) established
1577 the genus for endodontids displaying, among other features, (1) a large shell,
1578 (2) a narrow, U-shaped umbilicus, (3) a dome-shaped spire, (4) 3–4 large
1579 parietals and 4–5 large palatals, and (5) postnuclear major sculpture
1580 prominent to greatly reduced above periphery. To this genus, which
1581 originally comprised *K. callimus*, the type species, and *K. hypsus*, we added
1582 *K. cowiei*. *K. callimus* displays a unique combination of features that, in our

1583 view, justifies separation from *Mautodontha*. It has, for example, an
1584 adpressed apical suture, sculpture more prominent on the shell base than
1585 apically and an umbilicus that is constricted at the last whorl. *K. hypsus*
1586 and *K. cowiei* sp. nov., on the other hand, are not dissimilar in shell shape,
1587 umbilicus morphology and sculpture to certain species of *Mautodontha*
1588 (*Garrettoconcha*). They differ from the latter taxon mainly in their larger
1589 and more robust shells (Fig. 35). Hence, although we opted to retain
1590 *K. hypsus* and by extension *K. cowiei* sp. nov. in *Kleokyphus*, an alternative
1591 arrangement with these two species moved to *Mautodontha*
1592 (*Garrettoconcha*), thus restricting *Kleokyphus* to its type species, could be
1593 defended.

1594 The relationships of *Mautodontha* with other widespread genera,
1595 particularly *Minidonta* Solem, 1976 and *Australdonta* Solem, 1976, are
1596 poorly understood and require further study. These genera appear to be
1597 mainly characterized by plesiomorphic features and probably do not
1598 represent monophyletic groups. *Mautodontha* s.s. differs from the subgenus
1599 *Garrettoconcha* in having a wider umbilicus, lower spire, and apertural
1600 barriers that are more numerous and prominent. Among the new species
1601 established here, *M. (G.) occidentalis* sp. nov. and possibly
1602 *M. (G.) temaoensis* sp. nov. are smaller than the average *Garrettoconcha*,
1603 approaching in this respect the morphology of *Minidonta* (Fig. 35). Brook
1604 (2010, p. 194) briefly commented on the considerable morphological overlap
1605 between *Garrettoconcha* and *Minidonta*, and on the lack of consistent
1606 criteria for distinguishing the two. Nevertheless, in the absence of
1607 revisionary work at the generic level we preferred to follow Solem (1976) in
1608 regarding *Minidonta* and *Australdonta* as more southern genera, absent from
1609 Tuamotu and the Society Islands.

1610 Conservation status

1611 Of the thirteen major families of land snails native to the Pacific islands
1612 (Cowie 1996, table 1), Endodontidae may have been the most speciose
1613 (Solem 1976). However, very few of the more than two hundred known
1614 endodontid species have been found alive since the beginning of the 20th
1615 Century. For instance, intensive fieldwork carried out in the Gambier Islands
1616 in 1934 and 1997 recovered only empty shells of thirty endemic endodontid
1617 species, suggesting that they are all extinct (Abdou & Bouchet 2000). From
1618 Rurutu, Austral Islands, only one of nineteen endodontid species was
1619 collected alive in 1934, but none was found extant on the island in 2003,
1620 despite intensive surveying efforts (Zimmermann *et al.* 2009; Sartori *et al.*
1621 2013). And in Rarotonga, Cook Islands, Brook (2010) reported population
1622 decline of *Libera fratercula* (Pease, 1867) since the 1960s, with colonies
1623 surveyed in 2005–07 restricted to small remnants of native vegetation;
1624 among the other twelve Rarotongan endodontids, only one was possibly still
1625 extant in 2005–07 (Brook 2010).

1626 In the case of Makatea, *M. (M.) daedalea* may be the only survivor of an
1627 once richly diverse endodontid fauna. In 2005, only one extant population of
1628 this species was located in Makatea, on the coastal cliffs southeast of Moumu
1629 village (station Mk08). However, empty and worn shells of *M. (M.) daedalea*
1630 were numerous in almost every sampled locality (Fig. 39), suggesting a much
1631 wider former distribution. None of the other twenty-one species studied
1632 herein has ever been found alive and we cannot, therefore, refute the
1633 possibility that they are presently extinct.

1634 Nevertheless, the rugged terrain of Makatea, with thousands of deep pits
1635 left by the mining activities, represents a hindrance to field work on the

1636 island and we could not, unfortunately, sample in the south of the atoll.
1637 Lack of samples from the *Guettarda-Hernadia* forest (Fig. 2) is particularly
1638 frustrating, because this area concentrates the majority of the indigenous
1639 vascular plants of Makatea (Butaud & Jacq 2008) and presumably harbors
1640 the most suitable habitats for endodontids within the atoll. Hence,
1641 additional surveys of the malacofauna of Makatea, placing special emphasis
1642 on this area, are needed to determine whether additional colonies of
1643 *M. (M.) daedalea* and possibly other endodontids are extant in that forest.

1644 Even if some remnant populations still dwell in the atoll, it seems
1645 indisputable that a steep decline of the native endodontid fauna has
1646 occurred. However, the causes and timing of this decline are presently
1647 unknown. Habitat modification and destruction, predation by or
1648 competition with introduced species, and mortality from introduced
1649 pathogens are generally held responsible for recent extinctions of land snails
1650 of Pacific islands (e.g. Solem 1976, 1990; Preece 1998; Cowie &
1651 Grant-Mackie 2004). In Makatea, **exploitation** of phosphate deposits from
1652 1908 to 1966 dramatically changed the landscape of the atoll and much of its
1653 forest cover was burned during that time (Wilder 1934; Thibault & Guyot
1654 1987). Tempting as it may be to attribute the decline and extinction of the
1655 indigenous malacofauna of Makatea to the disturbances of this period,
1656 collections of land snails made before the onset of mining activities were too
1657 limited to provide a basis for comparison. Hence, at least some species may
1658 have been lost soon after initial human settlement, as has indeed occurred in
1659 other Pacific islands (e.g. Christensen & Kirch 1981; Preece 1998; Burney
1660 *et al.* 2001). Further studies of the malacofauna of Makatea, particularly
1661 additional field work in unexplored areas, archeological excavations and/or
1662 the direct dating of individual shells (Goodfriend 1989), are required to

1663 provide a chronology of the decline of endodontids on the atoll.

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Table 1. List of stations sampled in Makatea, French Polynesia, in 2005.

Station	Description
Mk01	Vaitepaua village (15.82155°S; 148.26622°W). Garden and deforested secondary zone. Limestone, alt. 60 m. 14/11/2005, coll. Gargominy & Fontaine.
Mk02	Wind turbine (15.83678°S; 148.25618°W). Summit of karst (feo). Limestone, alt. 55 m. 14/11/2005, coll. Gargominy & Fontaine.
Mk03	Road to Moumu, descending between cliffs (15.83496°S; 148.24928°W). Foot of the cliff. Limestone, alt. 50 m. 14/11/2005, coll. Gargominy & Fontaine.
Mk04	Moumu cave (15.83347°S; 148.24933°W). Deposits inside cave. Limestone, alt. 30 m. 14/11/2005, coll. Gargominy & Fontaine.
Mk05	Road to Moumu, descending between cliffs, top of the south cliff (15.83475°S; 148.24911°W). Summit of karst (feo). Limestone, alt. 55 m. 14/11/2005, coll. Gargominy & Fontaine.
Mk06	Southeast of Moumu, at the end of the beach (15.84004°S; 148.23091°W). Coastal cliff. <i>Scaevola</i> sp. Limestone, alt. 10 m. 15/11/2005, coll. Gargominy & Fontaine.
Mk07	Southeast of Moumu approximately 200 m before the end of the beach, slope under cliff (15.8408°S; 148.23315°W). Coconut trees, <i>Asplenium</i> sp. on rocks. Limestone, alt. 45 m. 15/11/2005, coll. Gargominy & Fontaine.
Mk08	Southeast of Moumu approximately 200 m before the end of the beach, halfway up the cliff (15.84094°S; 148.23303°W). Wet rocks. Limestone, alt. 60 m. 15/11/2005, coll. Gargominy & Fontaine.
Mk09	Coconut grove southeast of Moumu (15.83592°S; 148.24651°W). Inside cave. Limestone, alt. 5 m. 15/11/2005, coll. Gargominy & Fontaine.
Mk10	Coconut grove southeast of Moumu (15.83582°S; 148.24684°W). Inside cave. Limestone, alt. 5 m. 15/11/2005, coll. Gargominy & Fontaine.
Mk11	300 m. north of Temao port (15.82346°S; 148.27608°W). Degraded coastal forest at the bottom of cliff. Limestone, alt. 10 m. 16/11/2005, coll. Gargominy & Fontaine.
Mk12	Approximately 1 km. north of Temao port (15.81638°S; 148.27639°W). Large fault in the cliff, shaded. Ferns. Limestone, alt. 10 m. 16/11/2005, coll. Gargominy & Fontaine.
Mk13	West coast, approximately 3 km south of Temao (15.85189°S; 148.28018°W). Cave. Limestone, alt. 10 m. 17/11/2005, coll. Gargominy & Fontaine.
Mk14	West coast, approximately 3 km south of Temao (15.85189°S; 148.28018°W). Coastal forest. Bark with lichens. Limestone, alt. 10 m. 17/11/2005, coll. Gargominy & Fontaine.

Table 1. continued

Station	Description
Mk15	West coast approximately 1.5 km south of Temao (15.84151°S; 148.28076°W). Forest on karst (feo). <i>Asplenium</i> sp., <i>Ficus</i> sp. Limestone, alt. 20 m. 17/11/2005, coll. Gargominy & Fontaine.
Mk16	Road descending to Temao (15.82593°S; 148.27534°W). Lower side of the road below rocks. Limestone, alt. 10 m. 17/11/2005, coll. Gargominy & Fontaine.
Mk17	Mont Puutiare (15.81168°S; 148.26985°W). Phosphate mining ditch recolonized by vegetation. Limestone, alt. 100 m. 18/11/2005, coll. Gargominy & Fontaine.
Mk18	Coastal cliff north of Moumu (15.81626°S; 148.25756°W). Leaf litter beneath vegetation on rocks, accumulation area under cliff. Limestone, alt. 5m. 18/11/2005, coll. Gargominy & Fontaine.
Mk19	Coastal cliff north of Moumu (15.81782°S; 148.25673°W). Accumulation zone in rocky substratum. Limestone, alt. 10 m. 18/11/2005, coll. Gargominy & Fontaine.
Mk20	Plateau west of Anapoto (15.8406°S; 148.23141°W). Fault between rocks with coconut trees. Limestone, alt. 90 m. 19/11/2005, coll. Gargominy & Fontaine.
Mk21	Plateau west of Anapoto (15.8423°S; 148.22919°W). Fault between rocks. Limestone, alt. 90 m. 19/11/2005, coll. Gargominy & Fontaine.
Mk22	Plateau west of Anapoto (15.83987°S; 148.22852°W). Karst (feo) on top of cliff with <i>Ficus</i> sp. and <i>Pandanus</i> sp. Limestone, alt. 75 m. 19/11/2005, coll. Gargominy & Fontaine.
Mk23	Road between Vaitepaua and Moumu (15.82666°S; 148.26038°W). Bark of <i>Syzygium</i> sp. (Bladdernut). Limestone, alt. 55 m. 20/11/2005, coll. Gargominy & Fontaine.
Mk24	Road leading to the wind turbine (15.83597°S; 148.25307°W). Forest on karst (feo). Limestone, alt. 65 m. 20/11/2005, coll. Gargominy & Fontaine.
Mk25	South of the road leading to the wind turbine (15.83624°S; 148.2532°W). Exploited karst (feo), without vegetation. Limestone, alt. 56 m. 20/11/2005, coll. Gargominy & Fontaine.

Table 2. Dimensions (in mm) and ratios of specimens of *Mautodontha* (*Mautodontha*), *Mautodontha* (*Garrettoconcha*) and *Kleokyphus*. See Figure 3 for the placement of measurements. Abbreviations: ah, aperture height; aw, aperture width; d, shell diameter; h, shell height; rn, number of ribs on body whorl; sp, spire protrusion; u, diameter of umbilicus; wn, number of whorls.

Specimen	d	wn	rn	h	ah	aw	sp	u	h/d	ah/aw	u/d	sp/h
<i>M. (M.) daedalea</i>												
specimen 1 (Mk13)	3.69	5.55	154	1.49	1.00	1.27	0.29	1.31	0.40	0.79	0.36	0.20
specimen 2 (Mk13)	3.56	5.19	139	1.33	1.00	1.22	0.17	1.34	0.37	0.81	0.38	0.13
specimen 3 (Mk13)	3.66	5.68	152	1.50	0.98	1.21	0.34	1.36	0.41	0.81	0.37	0.23
specimen 4 (Mk13)	3.47	5.42	168	1.23	0.93	1.24	0.11	1.20	0.36	0.75	0.35	0.09
specimen 5 (Mk13)	3.47	5.49	115	1.30	1.05	1.24	0.11	1.23	0.37	0.84	0.35	0.09
specimen 6 (Mk13)	3.21	5.43	136	1.26	0.88	1.13	0.22	1.11	0.39	0.78	0.35	0.17
specimen 7 (Mk13)	3.20	5.35	128	1.26	0.90	1.13	0.19	1.08	0.39	0.79	0.34	0.15
specimen 8 (Mk13)	3.28	5.39	140	1.15	0.91	1.06	0.15	1.30	0.35	0.86	0.40	0.13
specimen 9 (Mk13)	3.10	6.35	165	1.36	0.99	0.99	0.20	1.16	0.44	0.99	0.37	0.14
specimen 10 (Mk13)	3.18	6.36	155	1.40	0.96	1.04	0.27	1.13	0.44	0.92	0.36	0.19
specimen 11 (Mk13)	3.17	6.04	147	1.28	0.99	0.97	0.14	1.24	0.41	1.02	0.39	0.11
specimen 12 (Mk13)	3.01	6.61	139	1.29	0.92	1.04	0.17	1.08	0.43	0.88	0.36	0.13
specimen 13 (Mk13)	3.10	6.12	155	1.27	1.03	1.00	0.19	1.18	0.41	1.03	0.38	0.15
specimen 14 (Mk13)	3.14	6.07	143	1.33	0.99	1.06	0.15	1.20	0.42	0.94	0.38	0.11
specimen 15 (Mk13)	2.91	6.22	156	1.25	0.96	1.01	0.14	1.10	0.43	0.94	0.38	0.11
specimen 16 (Mk13)	2.80	5.79	154	1.19	0.88	0.91	0.15	1.07	0.42	0.97	0.38	0.13
specimen 17 (Mk13)	2.92	5.93	114	1.30	0.89	1.04	0.18	1.06	0.45	0.85	0.36	0.14
specimen 18 (Mk22)	3.35	6.58	~160	1.55	1.15	1.26	0.23	0.97	0.46	0.91	0.29	0.15
specimen 19 (Mk22)	3.27	6.73	152	1.51	1.05	1.19	0.23	1.05	0.46	0.89	0.32	0.15
specimen 20 (Mk22)	3.35	6.30	~176	1.49	1.13	1.24	0.19	1.01	0.44	0.91	0.30	0.13
specimen 21 (Mk22)	3.19	6.52	~144	1.52	1.07	1.20	0.29	0.88	0.48	0.89	0.28	0.19
specimen 22 (Mk22)	2.98	6.15	147	1.27	1.01	1.08	0.13	1.00	0.43	0.94	0.34	0.10
specimen 23 (Mk22)	3.03	6.34	161	1.39	1.01	1.14	0.19	0.87	0.46	0.89	0.29	0.14
specimen 24 (Mk22)	3.11	6.21	~182	1.40	1.00	1.08	0.17	1.08	0.45	0.92	0.35	0.12
specimen 25 (Mk22)	2.94	6.15	133	1.33	0.98	1.10	0.20	0.87	0.45	0.89	0.30	0.15
specimen 26 (Mk22)	2.91	6.15	~148	1.30	0.98	1.08	0.18	0.87	0.45	0.91	0.30	0.14
mean	3.19	6.00	148.58	1.34	0.98	1.11	0.19	1.11	0.42	0.89	0.35	0.14
standard deviation	0.24	0.44	16.10	0.11	0.07	0.10	0.06	0.14	0.03	0.07	0.04	0.03
<i>M. (M.) domaneschii</i> sp. nov.												
holotype	3.14	5.00	61	1.36	0.78	1.08	0.18	1.24	0.43	0.72	0.39	0.13
paratype 1	3.05	5.07	75	1.46	0.78	1.03	0.24	1.05	0.48	0.76	0.35	0.16
paratype 2	3.18	4.95	74	1.42	0.78	1.07	0.25	1.15	0.45	0.73	0.36	0.18
paratype 3	3.10	5.27	70	1.58	0.81	1.07	0.41	1.02	0.51	0.76	0.33	0.26
paratype 4	3.11	5.23	64	1.37	0.78	1.03	0.23	1.16	0.44	0.76	0.37	0.17
paratype 5	2.84	5.13	67	1.25	0.70	0.92	0.16	0.99	0.44	0.76	0.35	0.13
paratype 6	3.20	5.67	70	1.64	0.80	1.01	0.41	1.13	0.51	0.79	0.35	0.25
paratype 7	3.03	5.21	75	1.45	0.79	1.07	0.29	1.01	0.48	0.74	0.33	0.20
paratype 8	3.06	4.55	71	1.29	0.84	1.00	0.12	1.03	0.42	0.84	0.34	0.09
mean	3.08	5.12	69.67	1.42	0.79	1.03	0.25	1.09	0.46	0.76	0.35	0.17
standard deviation	0.11	0.30	4.90	0.13	0.04	0.05	0.10	0.08	0.03	0.04	0.02	0.06

Table 2. continued

Specimen	d	wn	rn	h	ah	aw	sp	u	h/d	ah/aw	u/d	sp/h
<i>M. (M.) virginiae</i> sp. nov.												
holotype	3.56	6.30	75	2.02	1.21	1.38	0.45	0.97	0.57	0.87	0.27	0.22
paratype 1	3.69	6.48	90	2.12	1.15	1.38	0.65	1.01	0.57	0.83	0.27	0.31
paratype 2	3.63	6.05	101	2.03	1.12	1.46	0.58	0.85	0.56	0.77	0.24	0.28
paratype 3	3.50	6.12	91	1.74	1.12	1.28	0.33	1.00	0.50	0.88	0.29	0.19
paratype 4	3.39	5.96	98	1.76	1.17	1.28	0.44	0.97	0.52	0.91	0.29	0.25
paratype 5	3.42	5.99	89	1.67	1.12	1.25	0.35	1.04	0.49	0.89	0.31	0.21
paratype 6	3.40	5.70	96	1.71	1.21	1.26	0.26	1.05	0.50	0.96	0.31	0.15
paratype 7	3.26	5.82	102	1.55	1.04	1.14	0.29	1.01	0.48	0.92	0.31	0.19
paratype 8	3.37	5.99	89	1.64	1.21	1.15	0.30	1.13	0.49	1.05	0.34	0.18
mean	3.47	6.05	92.33	1.80	1.15	1.29	0.40	1.01	0.52	0.90	0.29	0.22
standard deviation	0.14	0.24	8.25	0.20	0.05	0.11	0.14	0.07	0.04	0.08	0.03	0.05
<i>M. (M.) harperae</i> sp. nov.												
holotype	3.50	5.64	141	1.88	1.22	1.23	0.48	1.27	0.54	0.99	0.36	0.26
paratype 1	3.34	5.30	159	1.78	1.21	1.26	0.33	0.97	0.53	0.95	0.29	0.19
paratype 2	3.11	5.52	153	1.66	1.04	1.20	0.34	0.99	0.53	0.86	0.32	0.21
paratype 3	3.06	-	135	1.61	1.08	1.17	0.31	0.91	0.53	0.93	0.30	0.19
paratype 4	2.86	4.63	150	1.35	1.17	1.09	0.17	0.83	0.47	1.07	0.29	0.13
paratype 5	2.91	4.69	153	1.41	1.07	1.10	0.26	0.79	0.48	0.97	0.27	0.19
paratype 6	2.61	4.25	127	1.21	1.05	0.95	0.16	0.83	0.46	1.10	0.32	0.14
mean	3.06	5.01	145.43	1.56	1.12	1.14	0.29	0.94	0.51	0.98	0.31	0.18
standard deviation	0.30	0.56	11.46	0.24	0.08	0.11	0.11	0.16	0.03	0.08	0.03	0.04
<i>M. (G.) aurora</i> sp. nov.												
holotype	3.05	5.60	176	1.80	1.02	1.31	0.43	0.55	0.59	0.78	0.18	0.24
paratype 1	2.87	4.99	123	1.58	1.00	1.21	0.30	0.61	0.55	0.83	0.21	0.19
paratype 2	2.94	5.04	136	1.65	1.01	1.24	0.33	0.65	0.56	0.81	0.22	0.20
paratype 3	3.23	5.56	163	1.98	0.99	1.27	0.63	0.66	0.61	0.78	0.20	0.32
paratype 4	3.05	5.52	143	1.87	0.94	1.22	0.53	0.63	0.61	0.77	0.21	0.28
paratype 5	3.01	5.27	144	1.77	0.96	1.20	0.51	0.73	0.59	0.80	0.24	0.29
paratype 6	3.02	5.18	138	1.73	1.03	1.22	0.44	0.62	0.57	0.85	0.20	0.25
paratype 7	2.95	5.13	134	1.72	1.02	1.15	0.37	0.69	0.58	0.89	0.23	0.21
paratype 8	2.96	5.17	145	1.72	0.96	1.23	0.38	0.69	0.58	0.78	0.23	0.22
mean	3.01	5.27	144.67	1.76	0.99	1.23	0.43	0.65	0.58	0.81	0.22	0.25
standard deviation	0.10	0.23	15.91	0.12	0.03	0.04	0.11	0.05	0.02	0.04	0.02	0.04
<i>M. (G.) occidentalis</i> sp. nov.												
holotype	2.40	5.59	154	1.71	0.81	0.99	0.57	0.52	0.71	0.82	0.21	0.34
paratype 1	2.46	5.20	149	1.57	0.88	0.96	0.44	0.63	0.64	0.91	0.26	0.28
paratype 2	2.48	5.24	173	1.48	0.85	0.98	0.37	0.67	0.60	0.87	0.27	0.25
paratype 3	2.28	5.38	133	1.45	0.85	0.92	0.39	0.57	0.64	0.92	0.25	0.27
paratype 4	2.20	5.30	139	1.43	0.81	0.92	0.39	0.42	0.65	0.89	0.19	0.27
paratype 5	2.20	5.25	143	1.91	0.97	1.20	0.58	0.45	0.87	0.81	0.21	0.31
paratype 6	2.15	5.25	153	1.51	0.88	0.90	0.42	0.40	0.70	0.97	0.19	0.28
paratype 7	2.06	5.42	118	1.43	0.79	0.87	0.42	0.39	0.69	0.91	0.19	0.30
paratype 8	2.11	5.01	150	1.42	0.78	0.86	0.42	0.47	0.67	0.91	0.22	0.30
mean	2.26	5.29	145.78	1.54	0.85	0.96	0.45	0.50	0.69	0.89	0.22	0.29
standard deviation	0.15	0.16	15.32	0.17	0.06	0.10	0.08	0.10	0.08	0.05	0.03	0.02

Table 2. continued

Specimen	d	wn	rn	h	ah	aw	sp	u	h/d	ah/aw	u/d	sp/h
<i>M. (G.) temaoensis</i> sp. nov.												
holotype	2.52	4.69	64	1.47	0.81	1.03	0.34	0.64	0.58	0.79	0.25	0.23
paratype 1	2.15	4.59	68	1.29	0.69	0.86	0.34	0.54	0.60	0.80	0.25	0.27
paratype 2	2.72	5.02	88	1.66	0.83	1.09	0.54	0.64	0.61	0.76	0.23	0.33
paratype 3	2.63	4.71	87	1.51	0.79	1.03	0.45	0.67	0.57	0.76	0.25	0.30
paratype 4	2.57	5.00	73	1.51	0.80	1.00	0.40	0.66	0.59	0.80	0.26	0.26
paratype 5	2.34	4.50	73	1.32	0.74	0.91	0.34	0.66	0.56	0.82	0.28	0.26
paratype 6	2.33	4.59	74	1.29	0.73	0.92	0.30	0.65	0.55	0.80	0.28	0.23
paratype 7	2.27	4.50	67	1.29	0.70	0.93	0.28	0.55	0.57	0.75	0.24	0.22
paratype 8	2.13	4.43	55	1.26	0.70	0.83	0.32	0.56	0.59	0.85	0.26	0.25
mean	2.41	4.67	72.11	1.40	0.76	0.96	0.37	0.62	0.58	0.79	0.26	0.26
standard deviation	0.21	0.21	10.49	0.14	0.05	0.09	0.08	0.05	0.02	0.03	0.02	0.03
<i>M. (G.) makateaensis</i> sp. nov.												
holotype	3.38	5.28	57	2.12	1.09	1.43	0.70	0.74	0.63	0.77	0.22	0.33
paratype 1	3.45	5.60	66	2.18	0.96	1.42	0.83	0.74	0.63	0.67	0.21	0.38
paratype 2	3.48	5.39	71	2.12	1.01	1.42	0.77	0.81	0.61	0.72	0.23	0.36
paratype 3	3.20	5.55	56	2.05	1.01	1.34	0.75	0.70	0.64	0.76	0.22	0.36
paratype 4	3.07	5.06	66	1.82	0.94	1.26	0.56	0.70	0.59	0.75	0.23	0.31
paratype 5	3.08	5.05	70	1.81	0.95	1.21	0.56	0.76	0.59	0.78	0.25	0.31
paratype 6	3.01	5.04	61	1.75	1.02	1.19	0.46	0.74	0.58	0.86	0.25	0.26
paratype 7	3.00	5.33	59	1.72	0.96	1.21	0.42	0.71	0.57	0.80	0.24	0.24
paratype 8	2.91	5.25	64	1.80	0.84	1.15	0.55	0.73	0.62	0.73	0.25	0.30
mean	3.18	5.28	63.33	1.93	0.98	1.29	0.62	0.74	0.61	0.76	0.23	0.32
standard deviation	0.21	0.21	5.43	0.18	0.07	0.11	0.15	0.03	0.02	0.05	0.01	0.05
<i>M. (G.) passosi</i> sp. nov.												
holotype	3.65	6.78	105	2.45	1.05	1.43	1.01	0.81	0.67	0.73	0.22	0.41
paratype 1	3.75	6.29	118	2.58	0.99	1.46	1.06	0.87	0.69	0.68	0.23	0.41
paratype 2	3.79	6.11	147	2.54	1.07	1.39	0.98	1.06	0.67	0.77	0.28	0.38
paratype 3	3.67	6.06	103	2.42	1.06	1.43	0.96	0.86	0.66	0.74	0.23	0.40
paratype 4	3.53	5.73	108	2.27	0.98	1.39	0.86	0.82	0.64	0.71	0.23	0.38
paratype 5	3.37	5.97	106	2.19	0.94	1.28	0.86	0.83	0.65	0.73	0.25	0.39
paratype 6	3.39	5.85	111	2.39	0.96	1.40	0.97	0.79	0.71	0.69	0.23	0.41
paratype 7	3.57	5.89	118	2.20	0.99	1.48	0.83	0.78	0.62	0.67	0.22	0.38
paratype 8	3.29	5.69	89	2.14	0.98	1.28	0.74	0.78	0.65	0.77	0.24	0.34
mean	3.56	6.04	111.67	2.35	1.00	1.39	0.92	0.84	0.66	0.72	0.24	0.39
standard deviation	0.18	0.33	15.84	0.16	0.05	0.07	0.10	0.09	0.03	0.04	0.02	0.02

Table 2. continued

Specimen	d	wn	rn	h	ah	aw	sp	u	h/d	ah/aw	u/d	sp/h
<i>M. (G.) spelunca</i> sp. nov.												
holotype	4.33	5.58	104	2.54	1.32	1.70	0.73	1.20	0.59	0.77	0.28	0.29
paratype 1	4.67	5.94	131	2.70	1.42	1.75	0.90	1.28	0.58	0.81	0.27	0.33
paratype 2	4.58	5.93	108	2.93	1.39	1.88	1.02	1.05	0.64	0.74	0.23	0.35
paratype 3	4.14	5.17	109	2.37	1.26	1.61	0.58	1.17	0.57	0.79	0.28	0.24
paratype 4	4.21	5.49	109	2.54	1.33	1.66	0.81	1.05	0.60	0.80	0.25	0.32
paratype 5	4.03	5.39	93	2.38	1.40	1.52	0.67	1.16	0.59	0.92	0.29	0.28
paratype 6	4.00	5.20	97	2.46	1.30	1.55	0.70	1.09	0.61	0.84	0.27	0.29
paratype 7	4.11	5.17	97	2.29	1.35	1.56	0.58	1.06	0.56	0.86	0.26	0.25
paratype 8	4.04	5.47	96	2.35	1.27	1.54	0.71	1.11	0.58	0.82	0.28	0.30
mean	4.23	5.48	104.89	2.51	1.34	1.64	0.74	1.13	0.59	0.82	0.27	0.29
standard deviation	0.25	0.30	11.57	0.20	0.06	0.12	0.15	0.08	0.02	0.05	0.02	0.03
<i>K. callimus</i>												
holotype	4.04	7.01	116	2.21	1.47	~1.54	0.32	0.75	0.55	0.96	0.19	0.14
paratype MNHN	4.44	7.40	~92	2.79	1.58	2.08	0.81	0.57	0.63	0.76	0.13	0.29
paratype FMNH	4.39	7.38	~104	2.51	1.62	2.07	0.53	0.69	0.57	0.78	0.16	0.21
paratype FMNH	3.68	6.65	~132	2.04	1.29	1.63	0.49	0.61	0.55	0.79	0.17	0.24
specimen 1	4.14	7.34	~160	2.50	1.38	1.81	0.73	0.69	0.60	0.76	0.17	0.29
specimen 2	3.90	7.12	~144	2.23	1.36	1.77	0.54	0.52	0.57	0.77	0.13	0.24
specimen 3	3.84	?	~100	2.22	1.33	1.70	0.51	0.70	0.58	0.78	0.18	0.23
specimen 4	3.60	?	94	1.90	1.19	1.55	0.33	0.72	0.53	0.77	0.20	0.18
specimen 5	3.12	6.09	99	1.54	1.14	1.31	0.21	0.73	0.49	0.87	0.23	0.14
mean	3.91	7.00	115.67	2.21	1.37	1.72	0.50	0.66	0.56	0.80	0.17	0.22
standard deviation	0.41	0.48	24.30	0.37	0.16	0.25	0.19	0.08	0.04	0.07	0.03	0.06
<i>K. hypsus</i>												
holotype	6.46	7.75	?	4.44	2.49	2.63	1.18	1.33	0.69	0.95	0.21	0.27
specimen 1	5.67	7.09	125	3.83	2.36	2.37	0.84	1.27	0.68	1.00	0.22	0.22
specimen 2	5.64	7.21	135	3.76	2.31	2.17	0.79	1.43	0.67	1.06	0.25	0.21
specimen 3	5.79	7.23	144	3.79	2.19	2.27	0.83	1.38	0.65	0.96	0.24	0.22
specimen 4	6.05	7.29	~132	3.91	2.53	2.34	0.73	1.60	0.65	1.08	0.26	0.19
specimen 5	5.25	6.99	130	3.26	2.12	2.07	0.62	1.22	0.62	1.03	0.23	0.19
specimen 6	5.42	6.68	140	3.51	2.21	2.21	0.66	1.21	0.65	1.00	0.22	0.19
specimen 7	5.07	6.77	123	3.27	2.02	2.06	0.73	1.28	0.65	0.98	0.25	0.22
specimen 8	3.06	5.18	109	1.75	1.35	1.24	0.25	0.82	0.57	1.09	0.27	0.14
mean	5.38	6.91	129.75	3.50	2.18	2.15	0.74	1.28	0.65	1.02	0.24	0.21
standard deviation	0.96	0.72	10.95	0.75	0.35	0.38	0.24	0.21	0.03	0.05	0.02	0.03

Table 2. continued

Specimen	d	wn	rn	h	ah	aw	sp	u	h/d	ah/aw	u/d	sp/h
<i>K. cowiei</i> sp. nov.												
holotype	4.47	6.47	~124	2.71	1.47	1.72	0.73	1.11	0.61	0.86	0.25	0.27
paratype 1	4.22	6.65	103	2.55	1.37	1.72	0.78	1.04	0.60	0.80	0.25	0.30
paratype 2	4.50	6.78	133	2.65	1.42	1.78	0.82	1.18	0.59	0.80	0.26	0.31
paratype 3	4.37	6.81	118	2.58	1.44	1.86	0.75	0.93	0.59	0.77	0.21	0.29
paratype 4	4.46	6.72	108	2.56	1.41	1.72	0.79	1.09	0.57	0.82	0.25	0.31
paratype 5	4.18	6.64	112	2.41	1.37	1.55	0.64	1.11	0.58	0.88	0.27	0.27
paratype 6	4.07	6.48	109	2.48	1.36	1.69	0.69	0.80	0.61	0.80	0.20	0.28
paratype 7	4.05	6.22	109	2.34	1.40	1.65	0.63	0.88	0.58	0.85	0.22	0.27
paratype 8	4.13	6.31	93	2.50	1.39	1.60	0.69	1.01	0.61	0.87	0.25	0.28
mean	4.27	6.56	112.11	2.53	1.40	1.70	0.72	1.02	0.59	0.83	0.24	0.29
standard deviation	0.18	0.21	11.71	0.11	0.04	0.09	0.06	0.12	0.01	0.04	0.02	0.02

Table 3. Dimensions (in mm) and ratios of specimens of *Pseudolibera*. See Figure 3 for the placement of measurements. Abbreviations: ah, aperture height; aw, aperture width; d, shell diameter; h, shell height; rn, number of ribs on body whorl; sp, spire protrusion; u, diameter of umbilicus; wn, number of whorls.

Specimen	d	wn	rn	h	ah	aw	sp	u	h/d	ah/aw	u/d	sp/h
<i>Pseudolibera lillianae</i>												
holotype	6.40	5.25	?	3.10	1.52	2.70	0.82	1.14	0.48	0.56	0.18	0.27
specimen 1	8.08	6.31	146	4.05	1.71	3.05	1.49	1.68	0.50	0.56	0.21	0.37
specimen 2	7.79	6.39	134	4.73	1.54	3.13	2.16	1.23	0.61	0.49	0.16	0.46
specimen 3	7.79	?	132	4.30	1.35	3.44	1.89	1.26	0.55	0.39	0.16	0.44
specimen 4	7.65	6.22	119	4.00	1.58	3.20	1.46	1.27	0.52	0.49	0.17	0.36
specimen 5	8.07	?	139	4.57	1.70	3.31	1.95	1.43	0.57	0.51	0.18	0.43
specimen 6	7.41	5.75	123	3.61	1.39	2.65	1.37	1.37	0.49	0.52	0.19	0.38
specimen 7	7.70	6.1	159	4.09	1.68	3.17	1.51	1.34	0.53	0.53	0.17	0.37
specimen 8	7.78	?	136	4.34	1.45	3.14	1.85	1.19	0.56	0.46	0.15	0.43
mean	7.63	6.00	136	4.09	1.55	3.09	1.61	1.32	0.53	0.50	0.17	0.39
standard deviation	0.50	0.43	12.63	0.50	0.13	0.26	0.40	0.16	0.04	0.05	0.02	0.06
<i>Pseudolibera solemi</i>												
holotype	6.45	6.55	126	4.17	1.74	3.25	1.47	0.96	0.65	0.53	0.15	0.35
paratype 1	6.94	6.97	~124	4.92	1.79	3.16	2.17	1.28	0.71	0.57	0.18	0.44
paratype 2	7.13	6.87	~132	4.29	1.66	3.27	1.76	1.03	0.60	0.51	0.14	0.41
paratype 3	6.87	6.84	~128	4.36	1.49	3.29	1.95	1.07	0.63	0.45	0.16	0.45
paratype 4	6.89	?	~156	4.87	1.47	3.00	2.31	1.25	0.71	0.49	0.18	0.47
paratype 5	6.83	6.66	~148	4.35	1.66	3.31	1.74	1.03	0.64	0.50	0.15	0.40
paratype 6	6.76	6.64	~104	4.38	1.60	3.06	1.85	1.15	0.65	0.52	0.17	0.42
paratype 7	7.02	6.72	~104	4.10	1.94	3.25	1.51	1.05	0.58	0.60	0.15	0.37
paratype 8	6.84	7.04	~136	4.76	1.74	3.13	2.04	1.09	0.70	0.55	0.16	0.43
mean	6.86	6.79	128.67	4.47	1.68	3.19	1.87	1.10	0.65	0.53	0.16	0.42
standard deviation	0.19	0.17	17.44	0.30	0.15	0.11	0.28	0.11	0.04	0.04	0.01	0.04
<i>Pseudolibera matthiewi</i>												
holotype	6.11	6.69	145	3.21	1.37	2.68	1.19	1.15	0.52	0.51	0.19	0.37
paratype 1	6.89	7.15	168	3.44	1.55	2.88	1.15	1.23	0.50	0.54	0.18	0.33
paratype 2	6.75	6.85	142	3.24	1.37	3.00	1.24	1.09	0.48	0.46	0.16	0.38
paratype 3	6.69	7.16	187	3.29	1.45	2.98	1.20	1.03	0.49	0.49	0.15	0.36
paratype 4	6.53	6.61	152	2.96	1.45	2.88	0.96	1.21	0.45	0.50	0.18	0.32
paratype 5	6.71	6.98	160	3.33	1.60	2.93	1.04	1.20	0.50	0.54	0.18	0.31
paratype 6	6.49	7.05	164	3.33	1.49	2.83	1.19	1.07	0.51	0.53	0.17	0.36
paratype 7	6.82	6.77	181	3.47	1.62	2.96	1.19	1.19	0.51	0.55	0.17	0.34
paratype 8	6.41	6.72	164	3.02	1.46	2.90	1.00	1.20	0.47	0.50	0.19	0.33
mean	6.60	6.89	162.56	3.25	1.48	2.89	1.13	1.15	0.49	0.51	0.17	0.35
standard deviation	0.24	0.21	15.08	0.17	0.09	0.10	0.10	0.07	0.02	0.03	0.01	0.02

Table 3. continued

Specimen	d	wn	rn	h	ah	aw	sp	u	h/d	ah/aw	u/d	sp/h
<i>Pseudolibera cookei</i>												
holotype	5.87	6.12	101	3.11	1.16	2.49	1.22	0.76	0.53	0.46	0.13	0.39
paratype 1	6.09	6.13	~92	3.60	1.32	2.48	1.53	0.87	0.59	0.53	0.14	0.43
paratype 2	6.06	5.78	?	3.24	1.23	3.07	1.09	0.74	0.53	0.40	0.12	0.34
paratype 3	5.61	5.68	99	3.24	1.21	2.50	1.27	0.71	0.58	0.48	0.13	0.39
paratype 4	5.58	5.72	78	2.99	1.32	2.59	1.09	0.65	0.54	0.51	0.12	0.36
paratype 5	6.29	5.16	68	3.20	1.54	2.76	0.97	1.34	0.51	0.56	0.21	0.30
paratype 6	6.31	?	~104	3.95	1.47	3.06	1.67	1.38	0.63	0.48	0.22	0.42
paratype 7	5.38	5.62	97	2.93	1.17	2.57	1.09	0.93	0.55	0.46	0.17	0.37
paratype 8	4.82	4.76	72	2.19	1.22	2.08	0.49	1.17	0.46	0.58	0.24	0.22
mean	5.78	5.62	88.88	3.16	1.29	2.62	1.16	0.95	0.54	0.50	0.16	0.36
standard deviation	0.48	0.46	14.11	0.48	0.13	0.31	0.34	0.28	0.05	0.06	0.05	0.06
<i>Pseudolibera aubertdelaruei</i>												
holotype	5.44	6.31	?	3.28	1.42	2.18	1.19	1.18	0.60	0.65	0.22	0.36
paratype 1	5.42	6.09	?	2.32	1.29	2.08	0.61	1.71	0.43	0.62	0.32	0.26
paratype 2	5.20	5.73	?	2.40	1.23	2.07	0.71	1.51	0.46	0.59	0.29	0.30
mean	5.35	6.04	?	2.67	1.31	2.11	0.84	1.46	0.50	0.62	0.27	0.31
standard deviation	0.14	0.29	?	0.53	0.10	0.06	0.31	0.27	0.09	0.03	0.05	0.05
<i>Pseudolibera extincta</i>												
holotype	6.40	6.81	220	3.31	1.23	2.58	1.13	1.37	0.52	0.48	0.21	0.34
paratype 1	6.45	7.05	210	3.40	1.26	2.52	1.27	1.39	0.53	0.50	0.22	0.37
paratype 2	6.09	6.93	~204	3.17	1.21	2.24	1.16	1.17	0.52	0.54	0.19	0.37
paratype 3	6.08	6.42	~192	3.12	1.27	2.22	1.16	1.33	0.51	0.57	0.22	0.37
paratype 4	6.19	6.98	~188	3.29	1.29	2.46	1.12	1.29	0.53	0.53	0.21	0.34
paratype 5	5.89	6.22	~160	3.07	1.11	2.24	1.24	1.22	0.52	0.50	0.21	0.40
paratype 6	6.02	6.80	228	3.19	1.10	2.32	1.21	1.27	0.53	0.48	0.21	0.38
paratype 7	5.89	6.80	214	3.00	1.01	2.17	1.16	1.25	0.51	0.47	0.21	0.39
paratype 8	5.85	6.73	237	3.10	1.27	2.56	1.06	1.25	0.53	0.50	0.21	0.34
mean	6.10	6.75	205.89	3.18	1.20	2.37	1.17	1.28	0.52	0.51	0.21	0.37
standard deviation	0.22	0.27	23.35	0.13	0.10	0.16	0.07	0.07	0.01	0.03	0.01	0.02
<i>Pseudolibera paraminderac</i>												
holotype	5.86	6.26	199	3.52	1.06	2.40	1.76	0.62	0.60	0.44	0.11	0.50
paratype 1	5.67	6.31	~160	3.26	1.01	2.21	1.53	1.09	0.58	0.46	0.19	0.47
paratype 2	5.73	5.96	~192	3.03	0.95	2.43	1.43	0.78	0.53	0.39	0.14	0.47
paratype 3	5.97	6.08	193	3.04	0.98	2.39	1.38	0.79	0.51	0.41	0.13	0.45
paratype 4	5.57	5.81	~162	3.00	0.86	2.35	1.38	0.58	0.54	0.36	0.10	0.46
paratype 5	5.47	6.02	237	2.98	0.96	2.35	1.45	0.79	0.54	0.41	0.14	0.49
paratype 6	5.49	6.12	198	3.20	0.98	2.34	1.58	0.86	0.58	0.42	0.16	0.49
paratype 7	5.50	6.58	~166	3.22	0.88	2.31	1.75	0.76	0.59	0.38	0.14	0.54
paratype 8	5.03	6.22	~202	2.99	0.93	1.75	1.48	1.11	0.59	0.53	0.22	0.49
mean	5.59	6.15	206.75	3.14	0.96	2.28	1.53	0.82	0.56	0.42	0.15	0.49
standard deviation	0.27	0.22	20.34	0.18	0.06	0.21	0.15	0.18	0.03	0.05	0.04	0.03

Table 3. continued

Specimen	d	wn	rn	h	ah	aw	sp	u	h/d	ah/aw	u/d	sp/h
<i>Pseudolibera elieporoi</i>												
holotype	6.28	7.13	104	4.79	1.63	2.86	2.48	0.92	0.76	0.57	0.15	0.52
paratype 1	6.19	6.64	76	3.94	1.42	2.81	1.77	1.02	0.64	0.50	0.16	0.45
paratype 2	6.73	?	156	4.53	1.77	2.52	2.04	1.46	0.67	0.71	0.22	0.45
paratype 3	6.44	6.71	95	4.15	1.63	2.63	1.60	1.31	0.64	0.62	0.20	0.38
paratype 4	6.23	6.69	93	4.08	1.40	2.63	1.65	1.11	0.65	0.53	0.18	0.40
paratype 5	6.46	6.97	77	4.16	1.46	2.62	1.76	1.36	0.64	0.56	0.21	0.42
paratype 6	6.17	6.16	85	4.32	1.45	2.43	2.03	1.17	0.70	0.59	0.19	0.47
paratype 7	6.15	6.78	88	4.27	1.39	2.66	1.87	0.85	0.69	0.52	0.14	0.44
paratype 8	6.00	6.70	97	4.21	1.50	2.78	1.94	1.08	0.70	0.54	0.18	0.46
mean	6.29	6.72	96.78	4.27	1.52	2.66	1.91	1.14	0.68	0.57	0.18	0.44
standard deviation	0.22	0.28	24.02	0.25	0.13	0.14	0.27	0.21	0.04	0.06	0.03	0.04
<i>Pseudolibera parva</i>												
holotype	3.26	5.08	72	1.86	0.74	1.32	0.65	0.81	0.57	0.56	0.25	0.35
paratype 1	3.40	5.03	74	1.85	0.76	1.38	0.70	0.82	0.54	0.55	0.24	0.38
paratype 2	3.28	4.73	75	1.69	0.71	1.28	0.46	0.83	0.52	0.56	0.25	0.27
paratype 3	3.29	4.49	78	1.57	0.80	1.20	0.35	0.95	0.48	0.67	0.29	0.22
paratype 4	3.30	4.72	89	1.64	0.78	1.24	0.46	0.97	0.50	0.63	0.29	0.28
paratype 5	3.22	4.55	59	1.55	0.68	1.33	0.38	0.77	0.48	0.51	0.24	0.25
paratype 6	3.39	4.53	59	1.54	0.76	1.27	0.34	1.07	0.45	0.59	0.31	0.22
paratype 7	3.21	4.52	69	1.47	0.80	?	0.28	0.94	0.46	?	0.29	0.19
paratype 8	3.17	4.25	~70	1.50	0.71	1.23	0.34	0.92	0.47	0.58	0.29	0.22
mean	3.28	4.66	71.67	1.63	0.75	1.28	0.44	0.90	0.50	0.58	0.27	0.26
standard deviation	0.08	0.27	9.27	0.14	0.04	0.06	0.15	0.10	0.04	0.05	0.03	0.06

Table 4. Endodontid species richness per island. Islands with less than three species of Endodontidae not shown. Data from: Solem (1976, 1983); Preece (1998); Abdou & Bouchet (2000); Brook (2010); Sartori *et al.* (2013).

Island	Island group	Endodontid species
Rapa	Austral Islands	24
Makatea	Tuamotu Archipelago	22
Mangareva	Gambier Islands	22
Rurutu	Austral Islands	19
Taravai	Gambier Islands	17
Aukena	Gambier Islands	15
Tahiti	Society Islands	14
Rarotonga	Cook Islands	14
Akamaru	Gambier Islands	11
Kauai	Hawaiian Islands	10
Oahu	Hawaiian Islands	8
Agakautai	Gambier Islands	8
Raivavae	Austral Islands	8
Nukuhiva	Marquesas	6
Hawaii	Hawaiian Islands	6
Hivaoa	Marquesas	5
Molokai	Hawaiian Islands	5
Raiatea	Society Islands	5
Moorea	Society Islands	5
Huahine	Society Islands	5
Borabora	Society Islands	5
Maui	Hawaiian Islands	4
Peleliu	Palau Islands	3
Tubuai	Austral Islands	3
Lanai	Hawaiian Islands	3
Aitutaki	Cook Islands	3



FIGURE 1. Topographic map showing the location of Makatea, in the northwestern part of the Tuamotu Archipelago. Map data by L. Claudel (Sardon - fr:Sardon) [GFDL (<http://www.gnu.org/copyleft/fdl.html>) or CC-BY-SA-3.0-2.5-2.0-1.0 (<http://creativecommons.org/licenses/by-sa/3.0>)], via Wikimedia Commons.

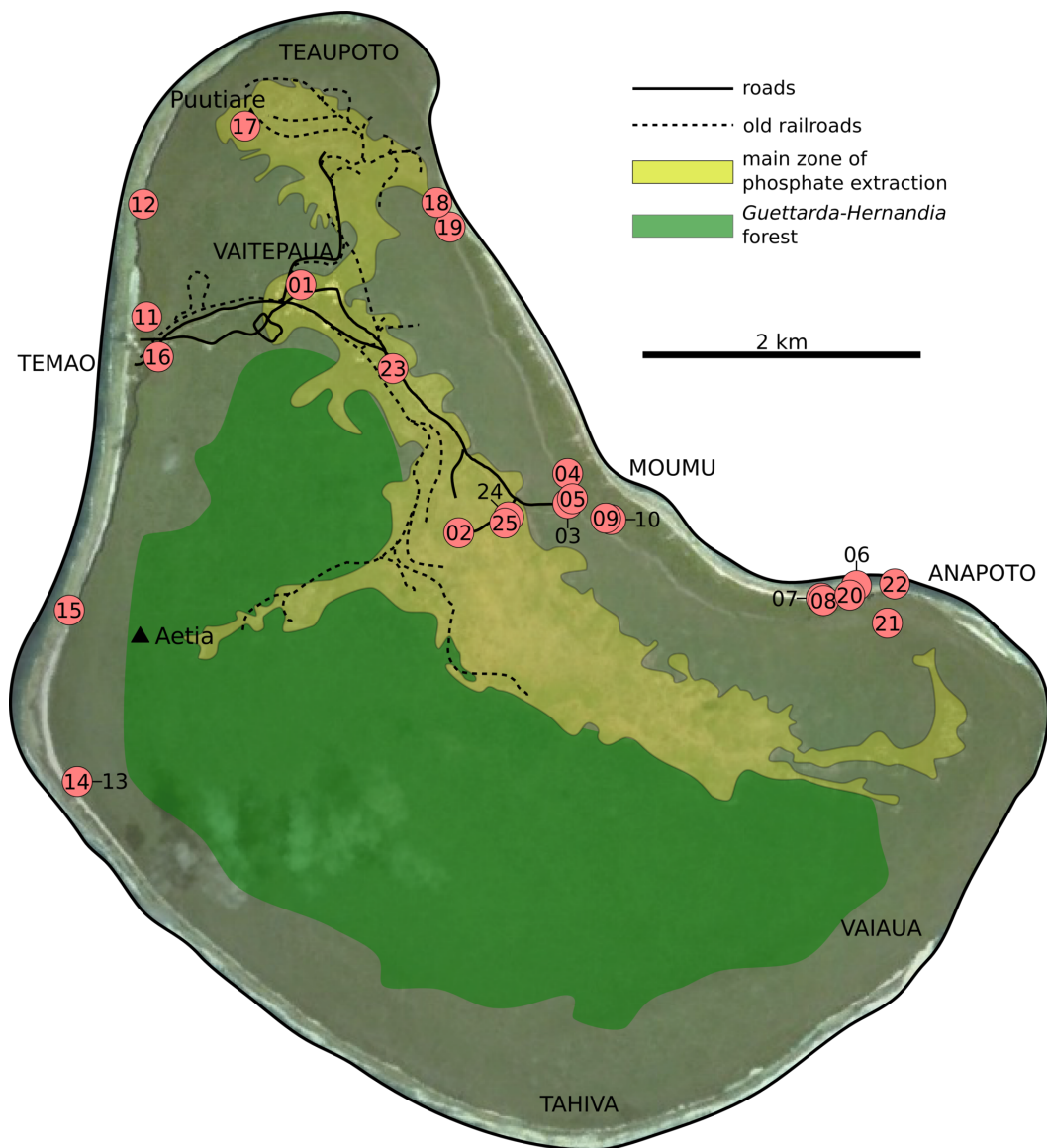


FIGURE 2. Map of Makatea (French Polynesia), showing the sampled localities. Map data: Google, DigitalGlobe, Butaud & Jacq (2008); Egretaud & Jouvin (2012).

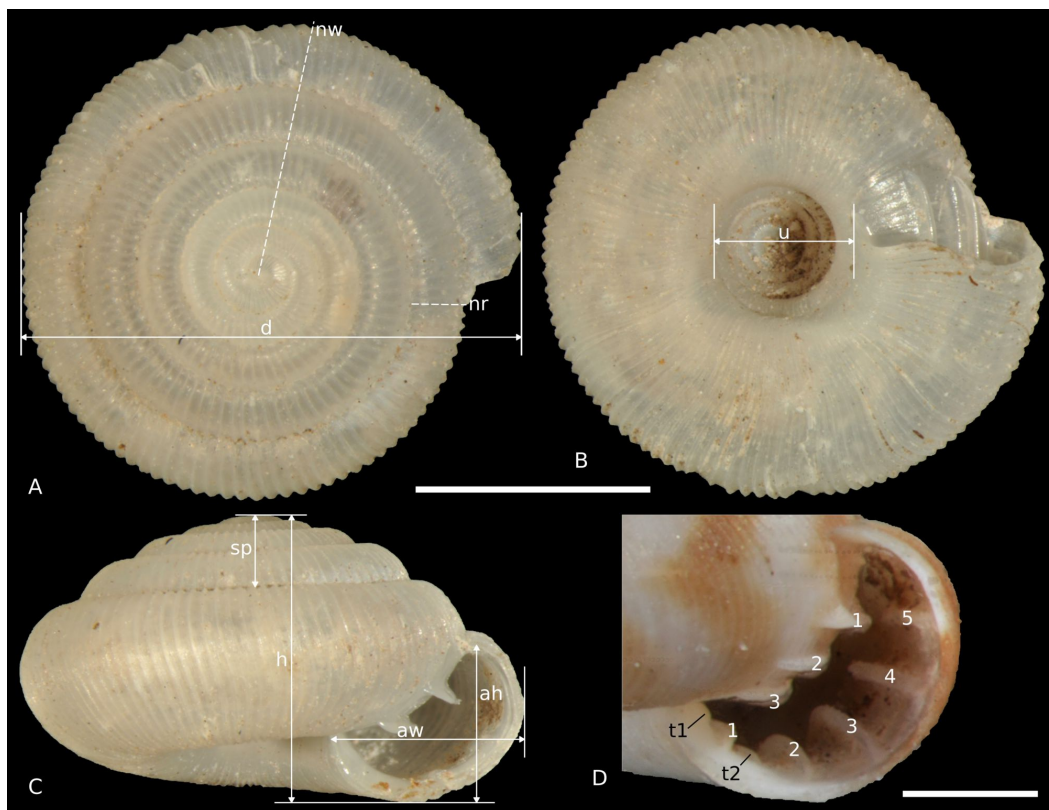


FIGURE 3. A–C. Photographs of *Mautodontha* (*Garrettoconcha*) *spelunca* sp. nov. (MNHN 25583, paratype 3), showing the placement of measurements used in this study; D. Peristome of *Mautodontha* (*Mautodontha*) *daedalea* (MNHN 25587, specimen 9), showing the numbering scheme for apertural barriers used in this study. Abbreviations: ah, aperture height; aw, aperture width; d, shell diameter; h, shell height; nr, number of ribs on body whorl (counted from this line to the aperture); nw, number of whorls (line marks the boundary between whorls); sp, spire protrusion; t1,t2, barrier traces; u, umbilicus diameter. Scale bars: A–C = 2 mm; D = 0.5 mm.

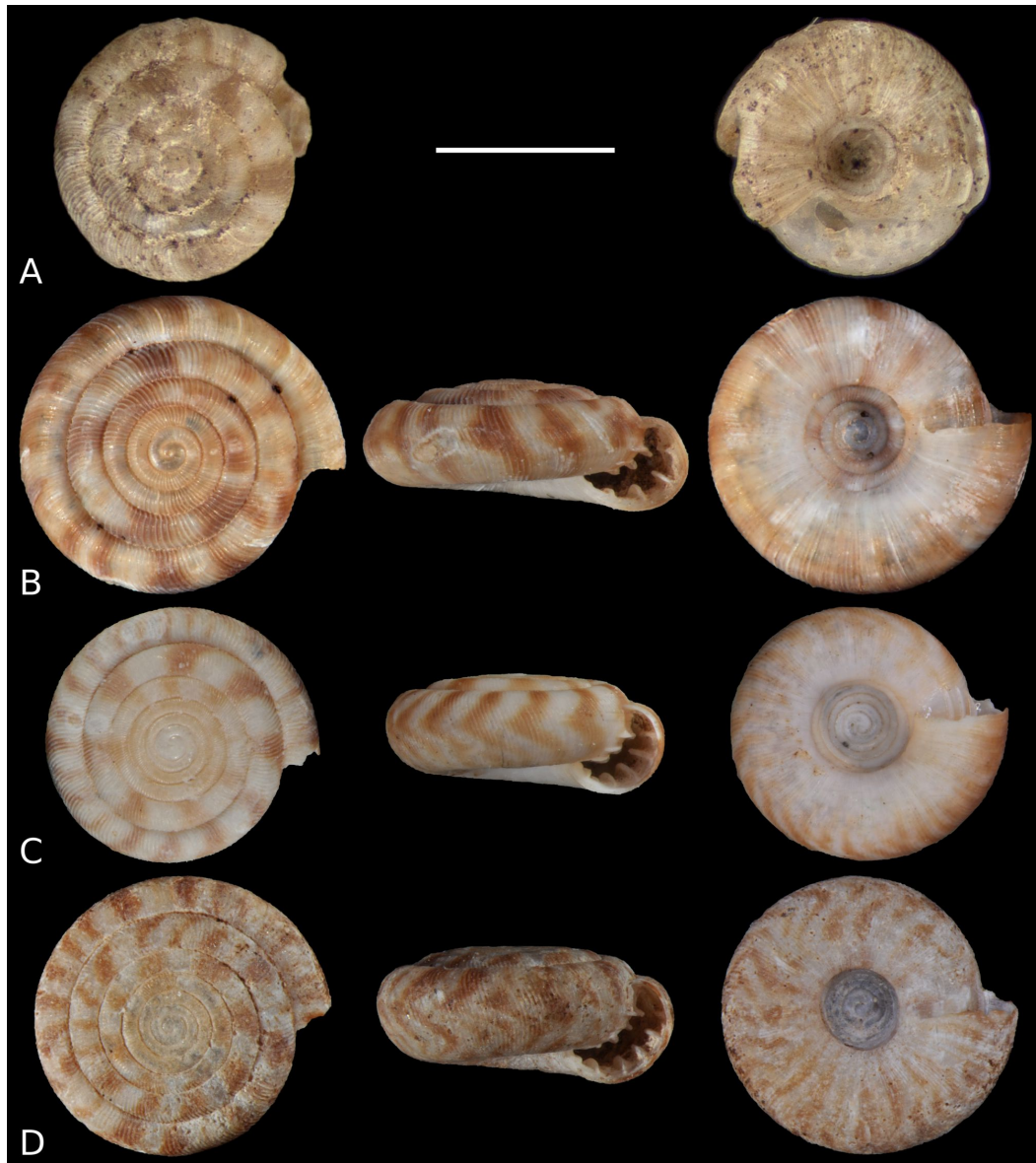


FIGURE 4. *Mautodontha (Mautodontha) daedalea*. **A.** Lectotype (MCZ 169115); **B.** Specimen 1 (station Mk13); **C.** Specimen 9 (MNHN 25587, station Mk13); **D.** Specimen 18 (station Mk22); Scale bar = 2 mm.

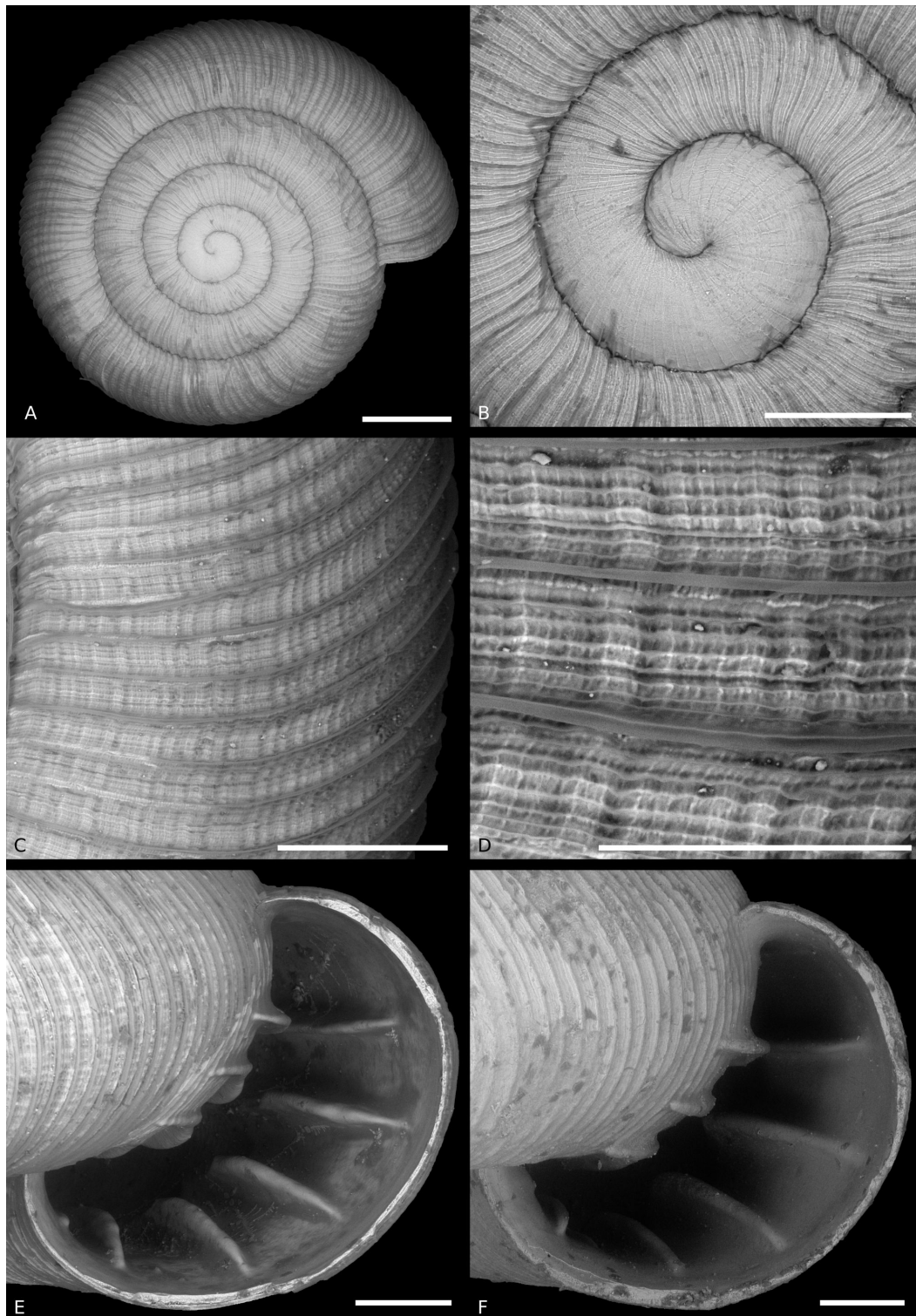


FIGURE 5. *Mautodontha (Mautodontha) daedalea*. **A–C.** MNHN 25584 (specimen 27, station Mk08), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Detail of the sculpture of the late teleoconch; **E.** MNHN 25584 (specimen 28, station Mk08), detail of the peristome; **F.** MNHN 25587 (specimen 9, station Mk13), detail of the peristome; Scale bars: A = 0.5 mm; B,C,E,F = 0.2 mm; D = 0.1 mm.

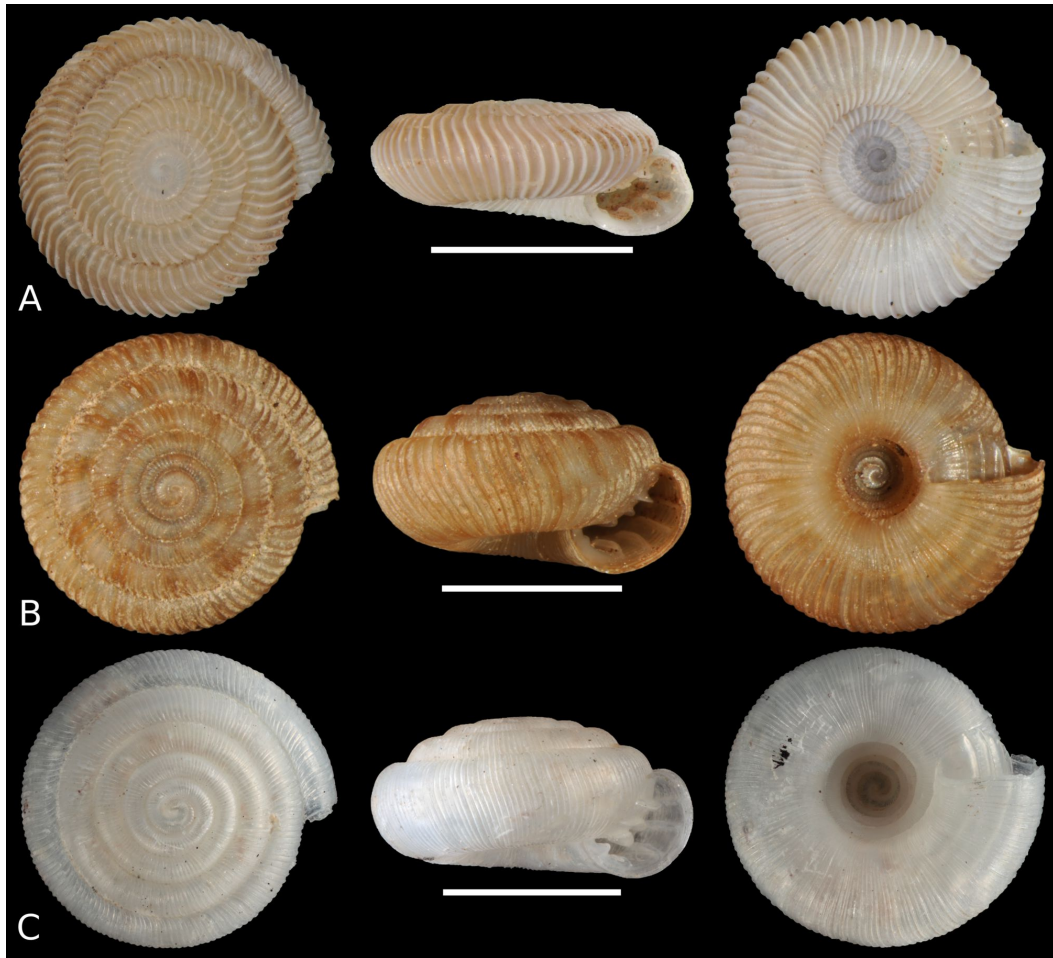


FIGURE 6. Holotypes of: **A.** *Mautodontha (Mautodontha) domaneschii* sp. nov.; **B.** *Mautodontha (Mautodontha) virginiae* sp. nov.; **C.** *Mautodontha (Mautodontha) harperae* sp. nov. Scale bars = 2 mm.

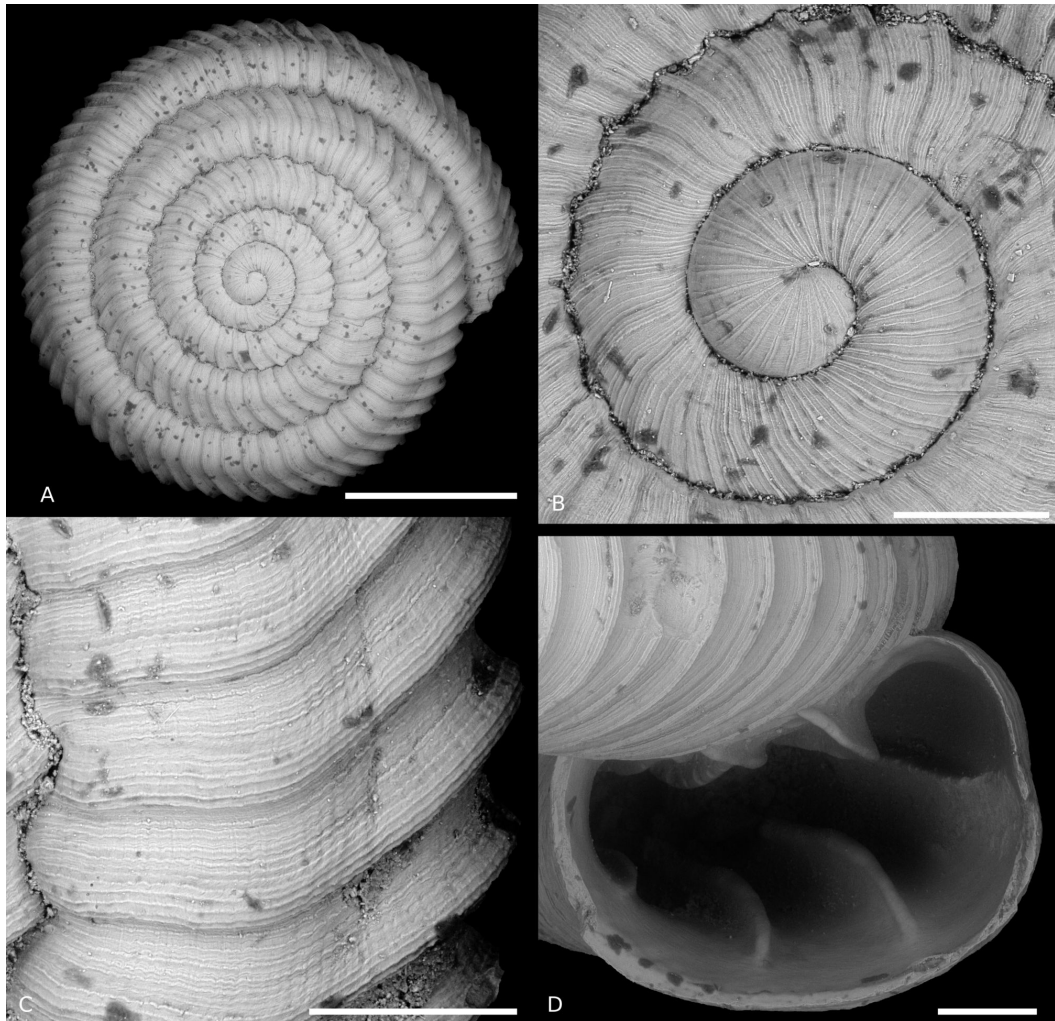


FIGURE 7. *Mautodontha (Mautodontha) domaneschii* sp. nov. **A–C.** Holotype (MNHN 25585), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 1 (MNHN 25586), detail of the peristome; Scale bars: A = 1 mm; B–D = 0.2 mm.

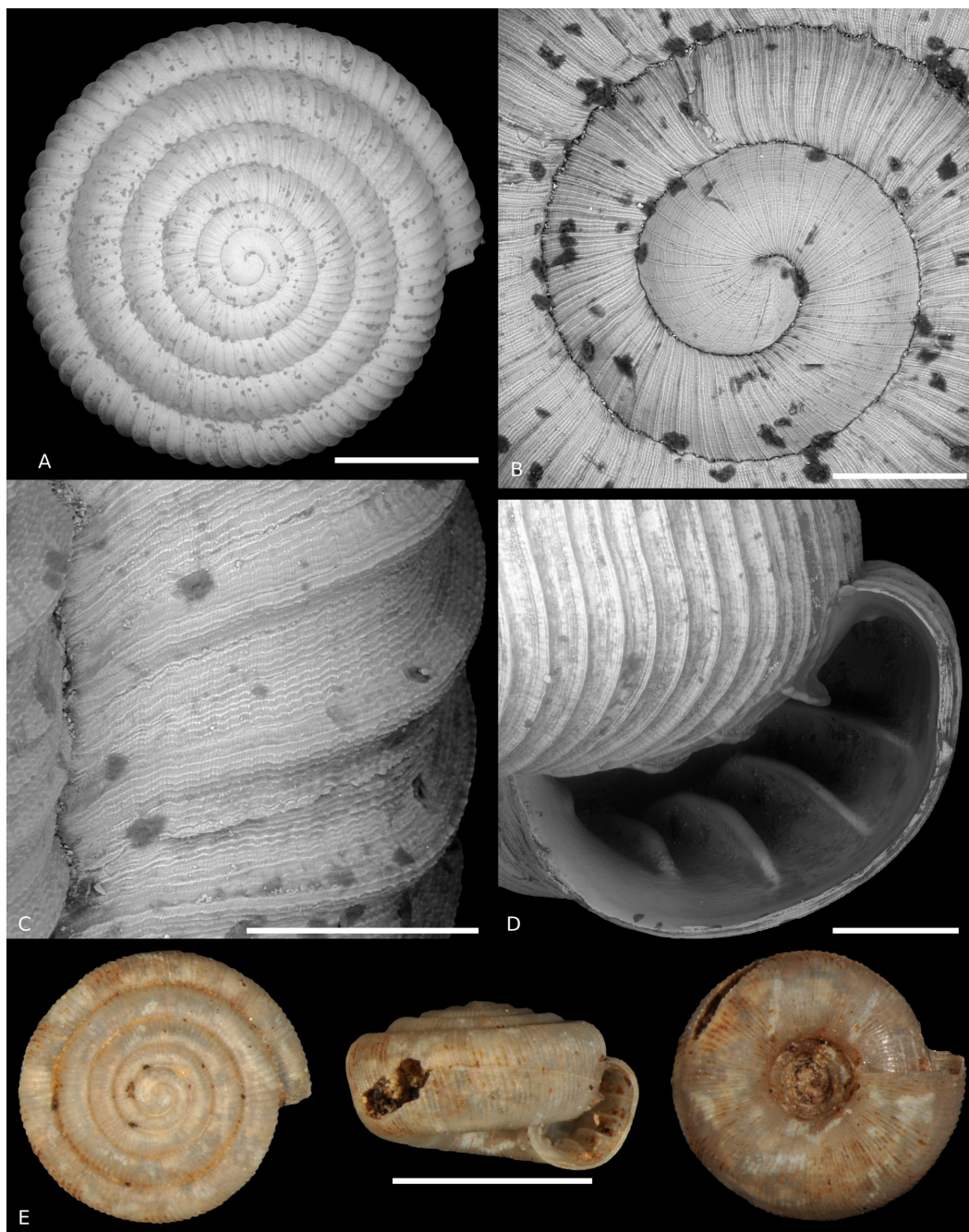


FIGURE 8. *Mautodontha (Mautodontha) virginiae* sp. nov. **A–C.** Holotype (MNHN 25681), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 1 (MNHN 25682), detail of the peristome; **E.** Aberrant specimen (MNHN 25686) from station Mk18; Scale bars: A = 1 mm; B–C = 0.2 mm; D = 0.4 mm; E = 2 mm.

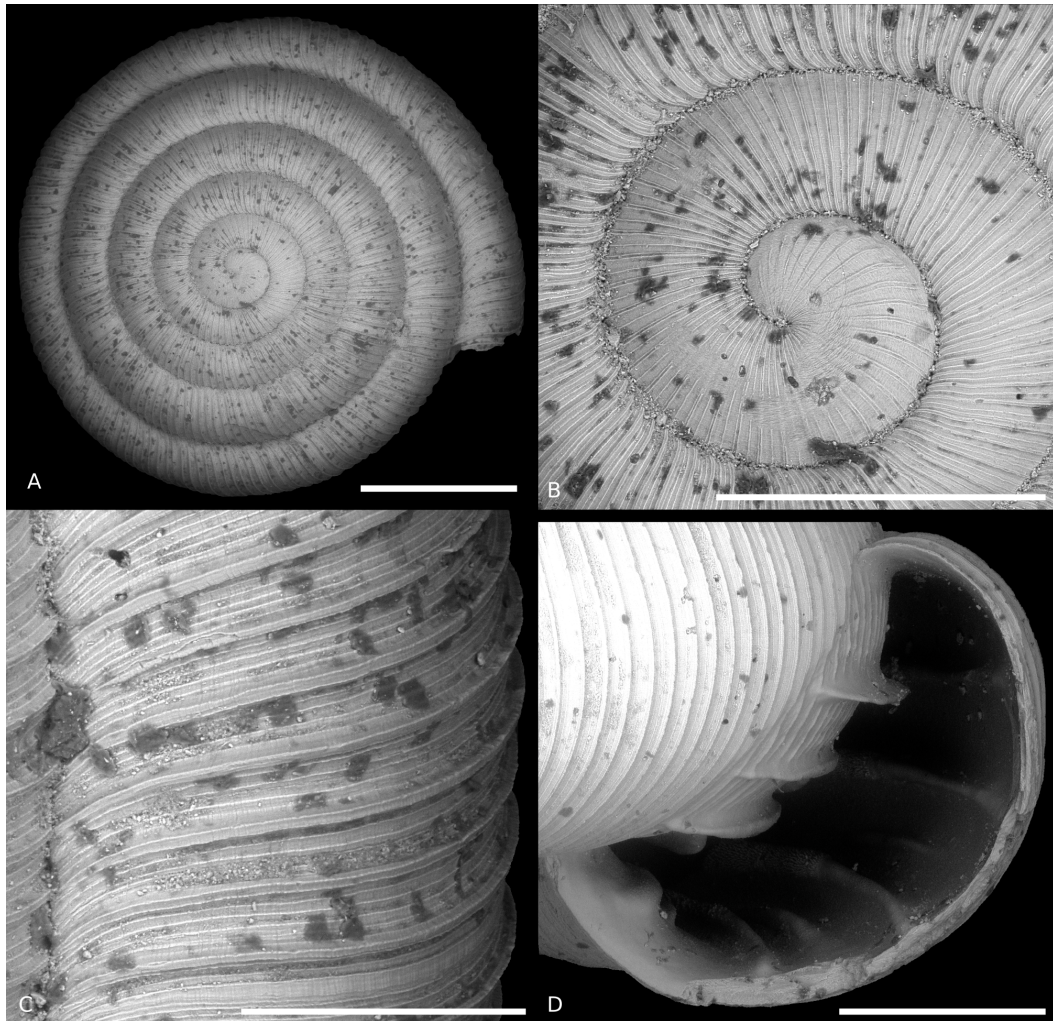


FIGURE 9. *Mautodontha (Mautodontha) harperae* sp. nov. **A–C.** Holotype (MNHN 26529), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 1 (MNHN 26530), detail of the peristome; Scale bars: A = 1 mm; B,D = 0.5 mm; C = 0.25 mm.

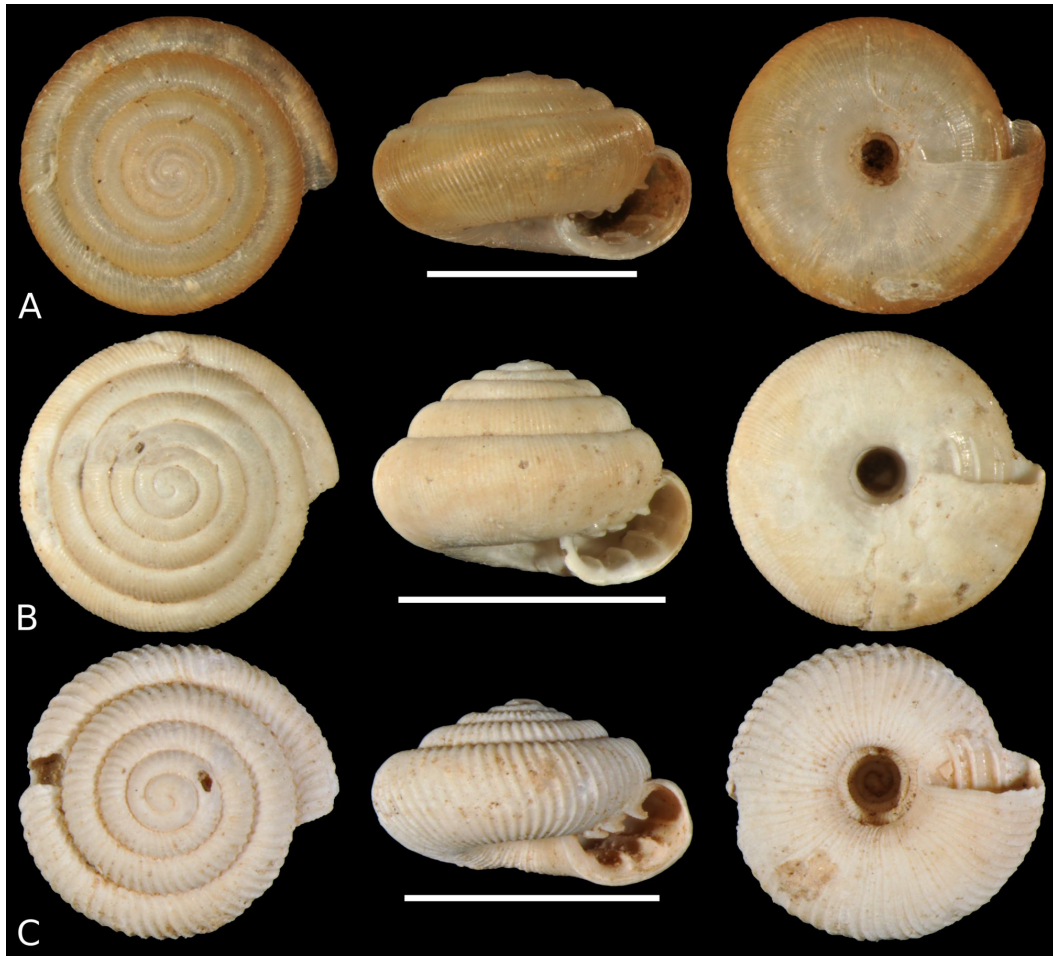


FIGURE 10. Holotypes of: **A.** *Mautodontha* (*Garrettoconcha*) *aurora* sp. nov.; **B.** *M.* (*G.*) *occidentalis* sp. nov.; **C.** *M.* (*G.*) *temaoensis* sp. nov.. Scale bars = 2 mm.

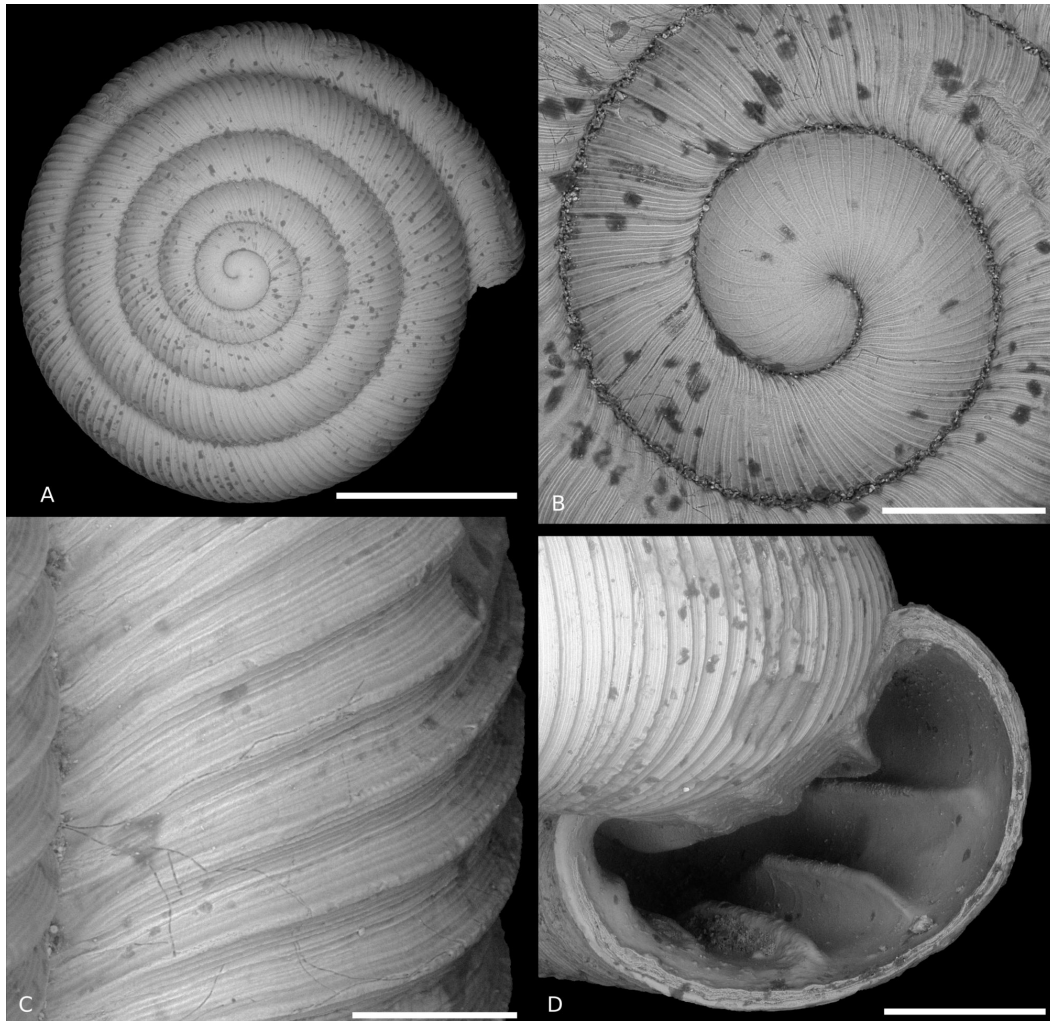


FIGURE 11. *Mautodontha* (*Garrettoconcha*) *aurora* sp. nov. **A–C.** Holotype (MNHN 25575), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 1 (MNHN 25576), detail of the peristome. Scale bars: A = 1 mm; B = 0.2 mm; C = 0.1 mm; D = 0.4 mm.

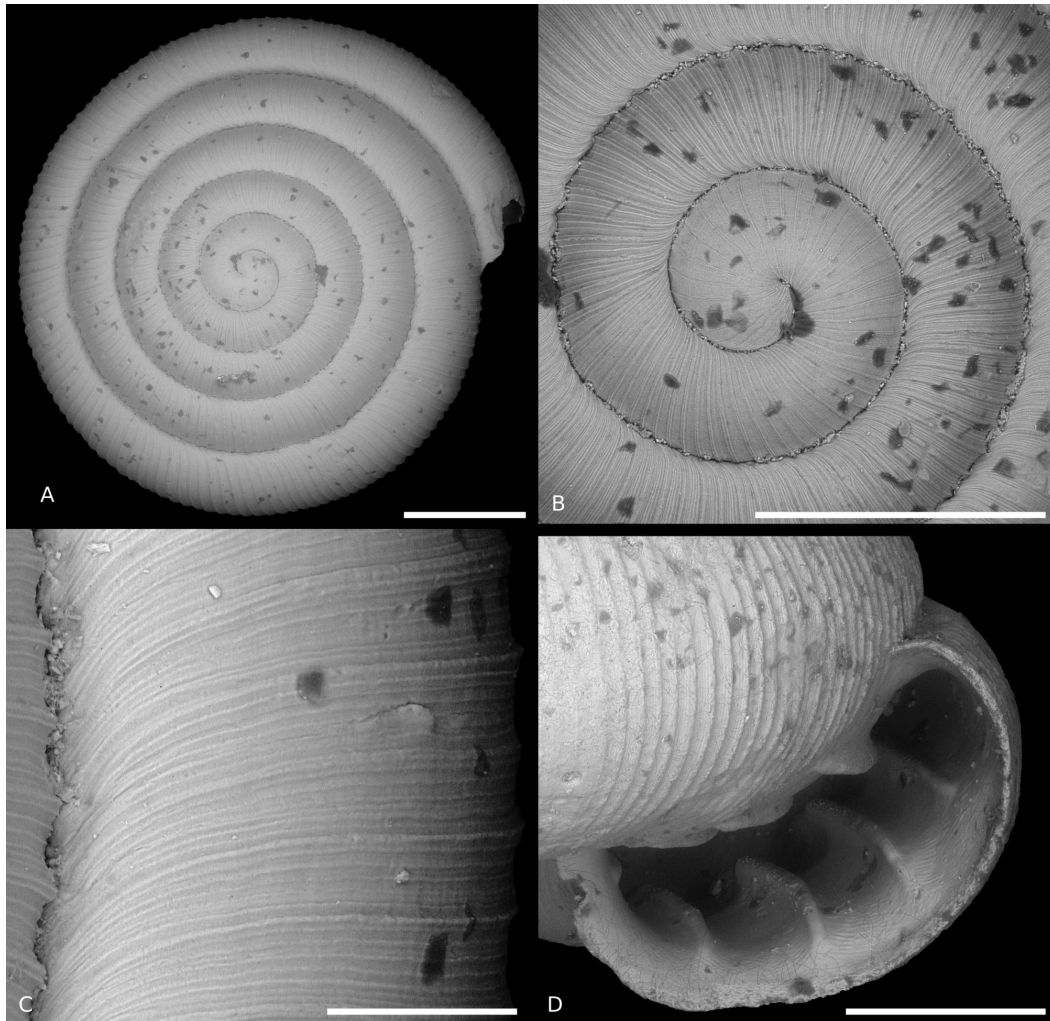


FIGURE 12. *Mautodontha* (*Garrettoconcha*) *occidentalis* sp. nov. **A–C.** Paratype 3 (MNHN 25574), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Holotype (MNHN 25573), detail of the peristome; Scale bars: A = 0.5 mm; B,D = 0.4 mm; C = 0.1 mm.

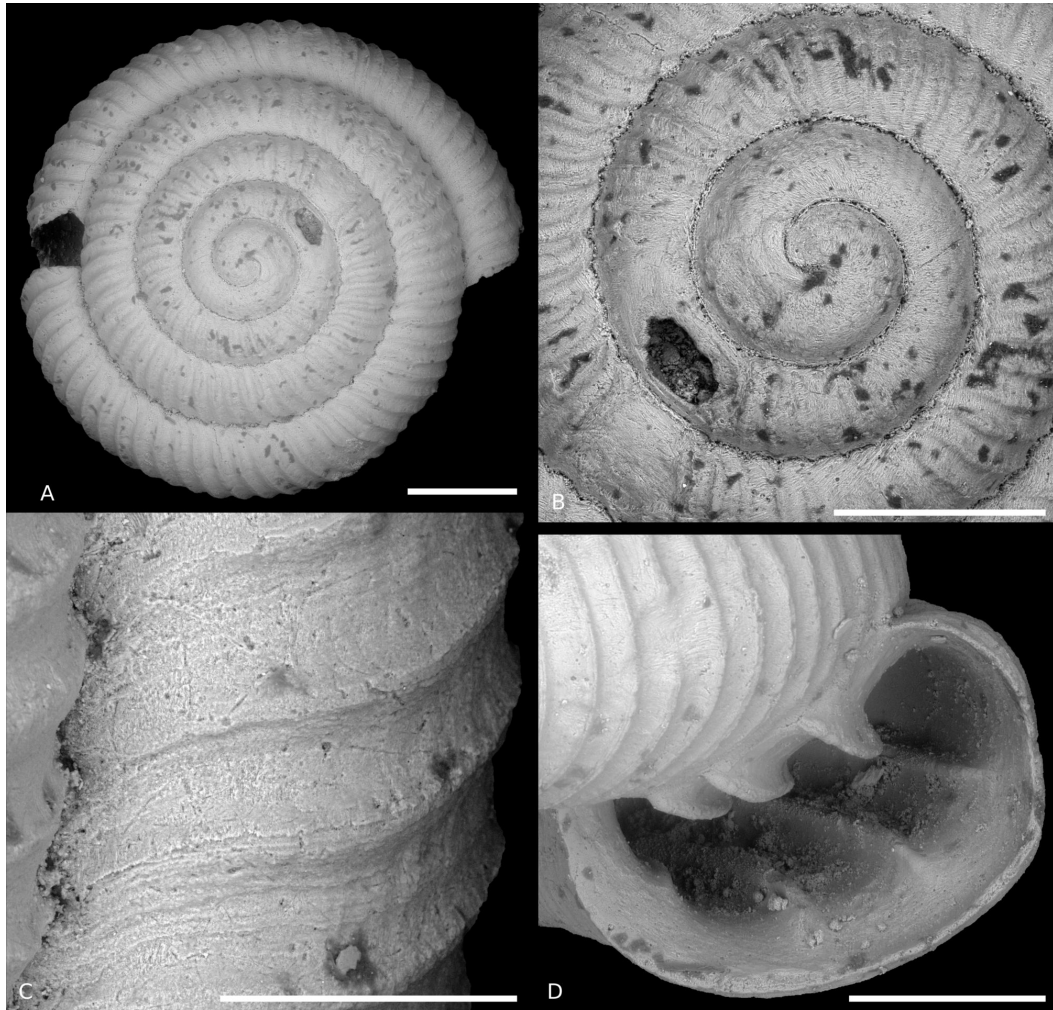


FIGURE 13. *Mautodontha* (*Garrettoconcha*) *temaoensis* sp. nov. Holotype (MNHN 25685) **A–C.** Apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Detail of the peristome. Scale bars: A = 0.5 mm; B,D = 0.4 mm; C = 0.2 mm.



FIGURE 14. Holotypes of: **A.** *Mautodontha (Garrettoconcha) makateaensis* sp. nov.; **B.** *M. (G.) passosi* sp. nov.; **C.** *M. (G.) spelunca* sp. nov.. Scale bars = 2 mm.

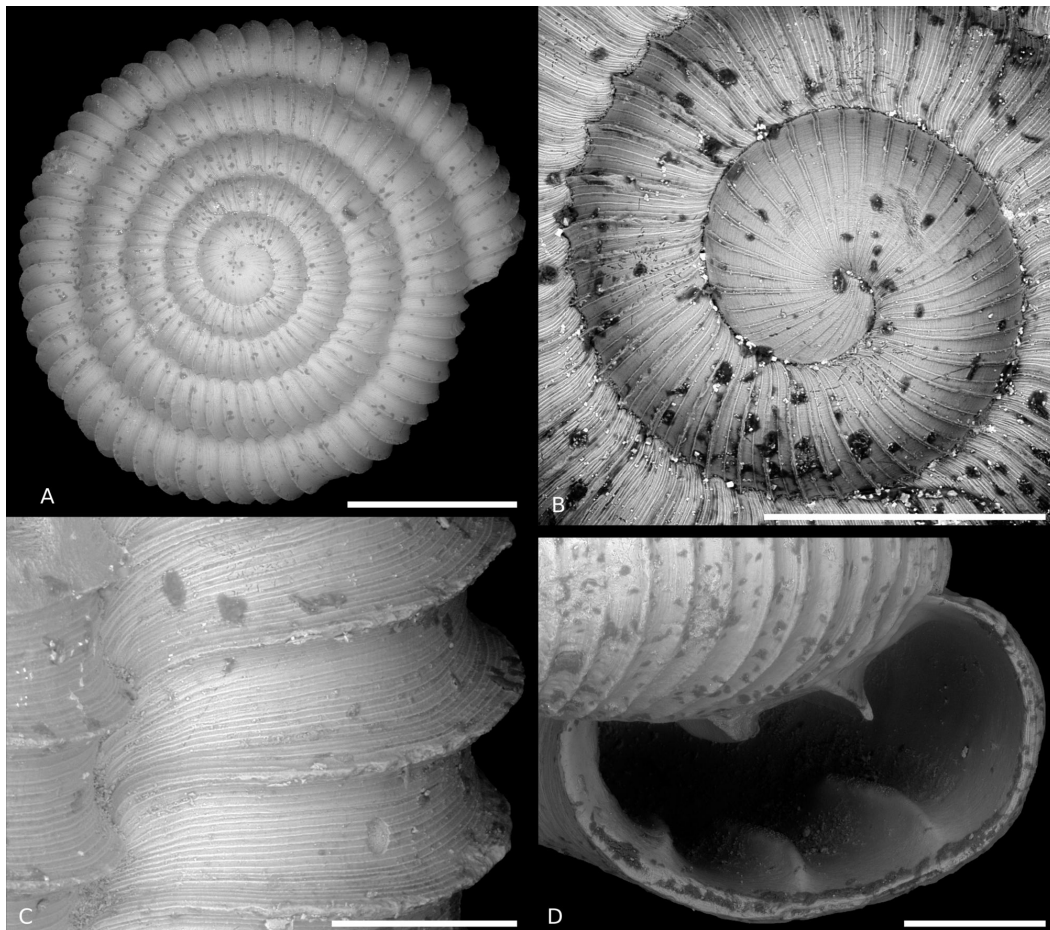


FIGURE 15. *Mautodontha* (*Garrettoconcha*) *makateaensis* sp. nov. **A–C.** Holotype (MNHN 25683), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 2 (MNHN 25684), detail of the peristome; Scale bars: A = 1 mm; B,D = 0.4 mm; C = 0.2 mm.

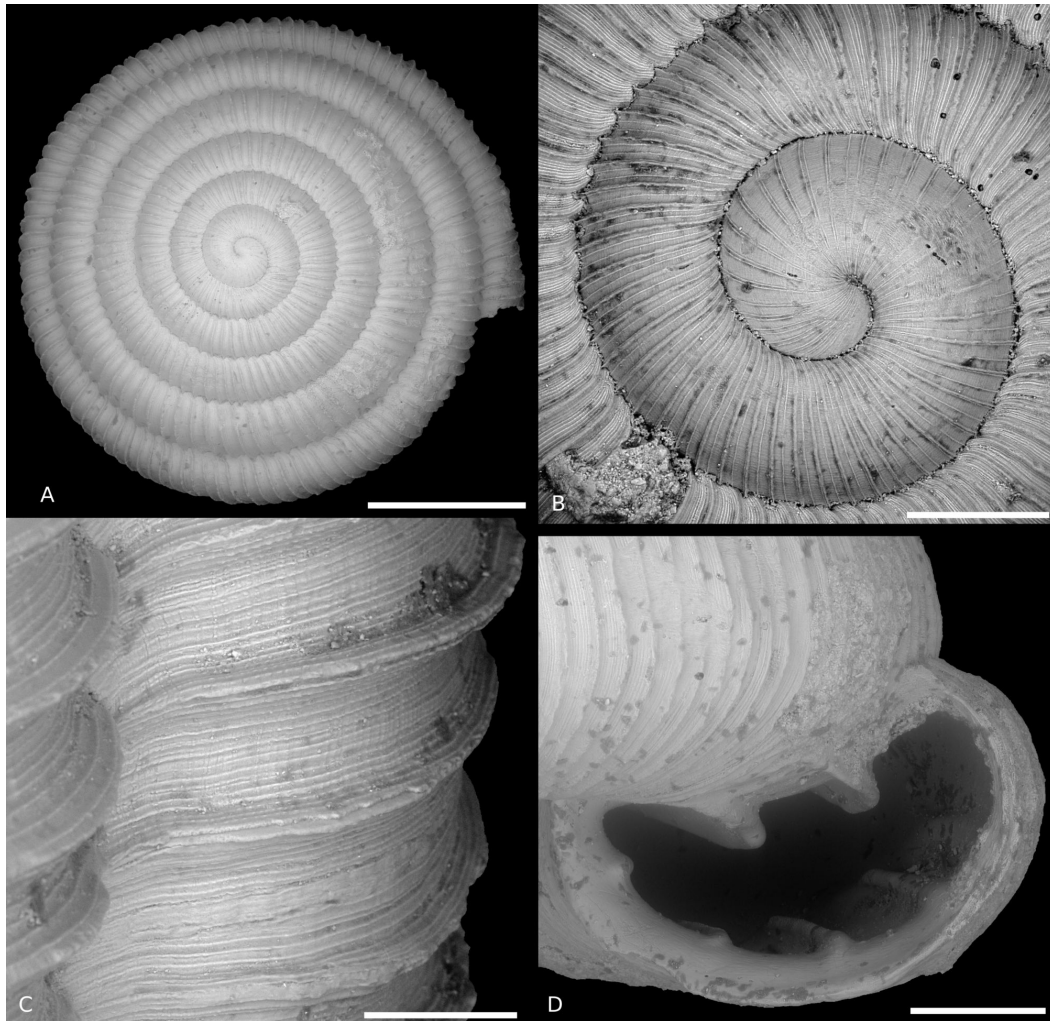


FIGURE 16. *Mautodontha* (*Garrettoconcha*) *passosi* sp. nov. **A–C.** Holotype (MNHN 25578), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 1 (MNHN 25579), detail of the peristome; Scale bars: A = 1 mm; B,D = 0.2 mm; C = 0.1 mm.

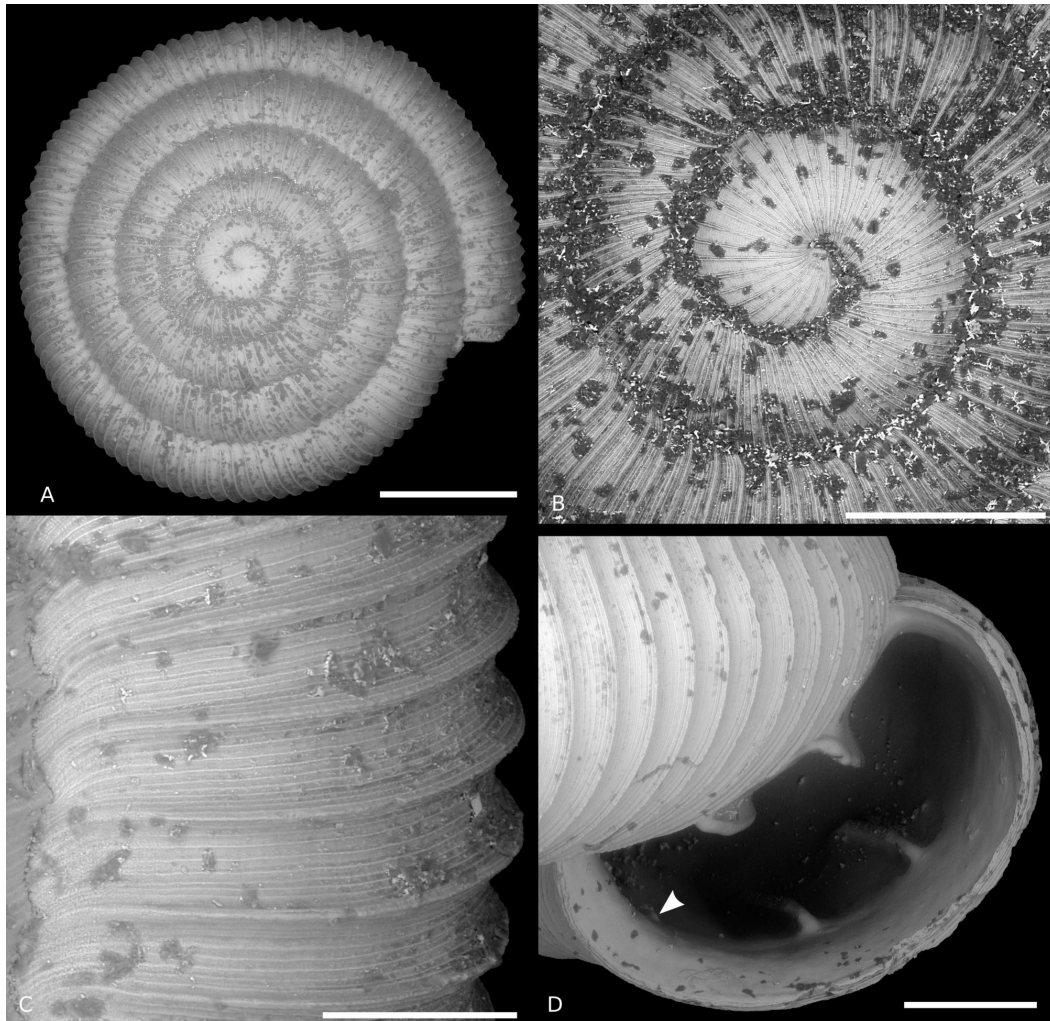


FIGURE 17. *Mautodontha* (*Garrettoconcha*) *spelunca* sp. nov. **A–C.** Paratype 3 (MNHN 25583), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 8 (MNHN 25583), detail of the peristome (arrowhead indicates palatal 1); Scale bars: A = 1 mm; B,D = 0.4 mm; C = 0.2 mm.



FIGURE 18. *Kleokyphus callimus*; **A.** Holotype (MNHN 25568); **B.** Paratype (MNHN 25569); Scale bars = 2 mm.

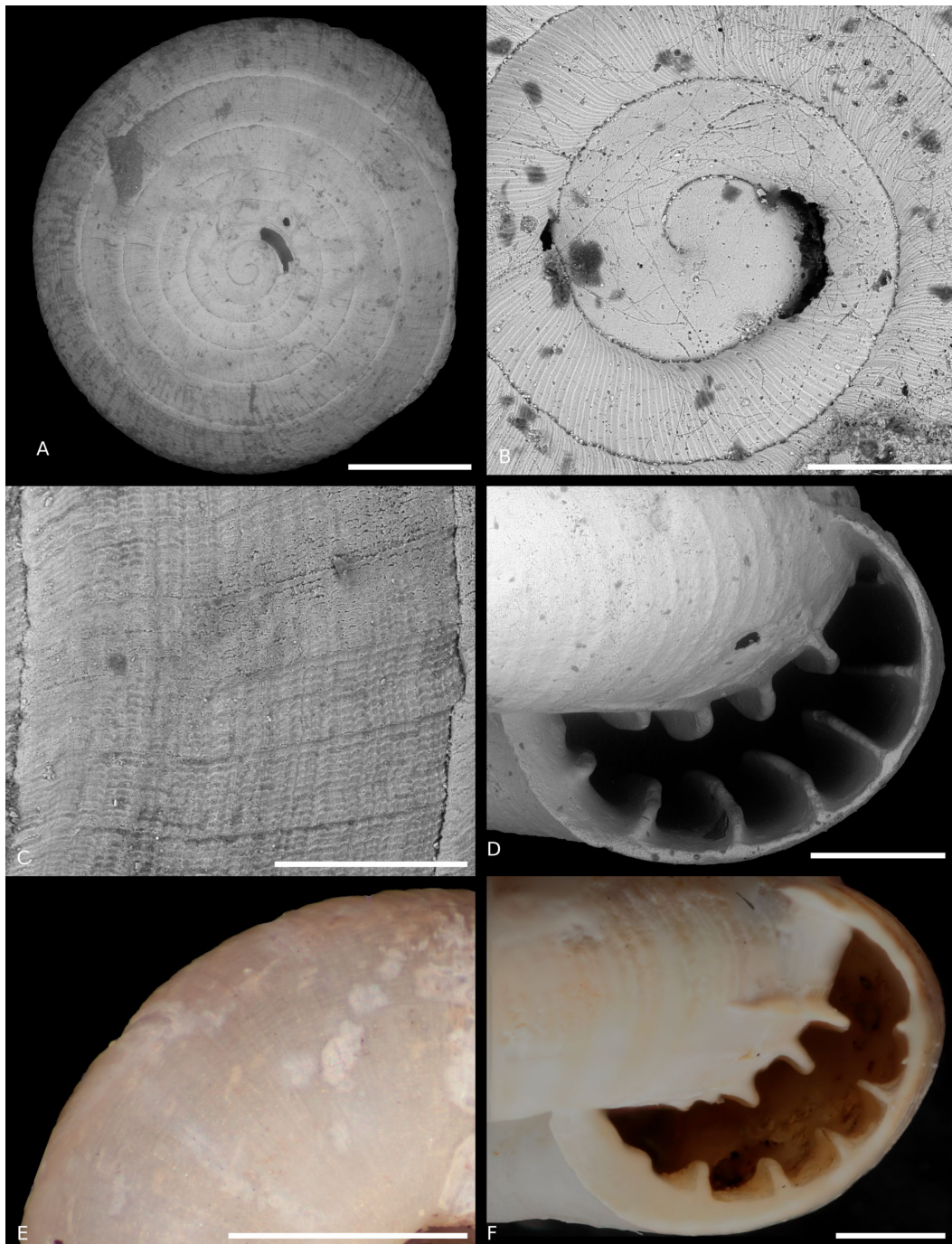


FIGURE 19. *Kleokyphus callimus* A–C. Holotype (MNHN 25568), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Specimen 3 (MNHN 25570), detail of the peristome; **E.** Paratype (FMNH 153781), showing spiral cording on the shell base; **F.** Specimen 1 (MNHN 25570), detail of the peristome; Scale bars: A,E = 1 mm; B,C = 0.2 mm; D,F = 0.5 mm; E = 1 mm.

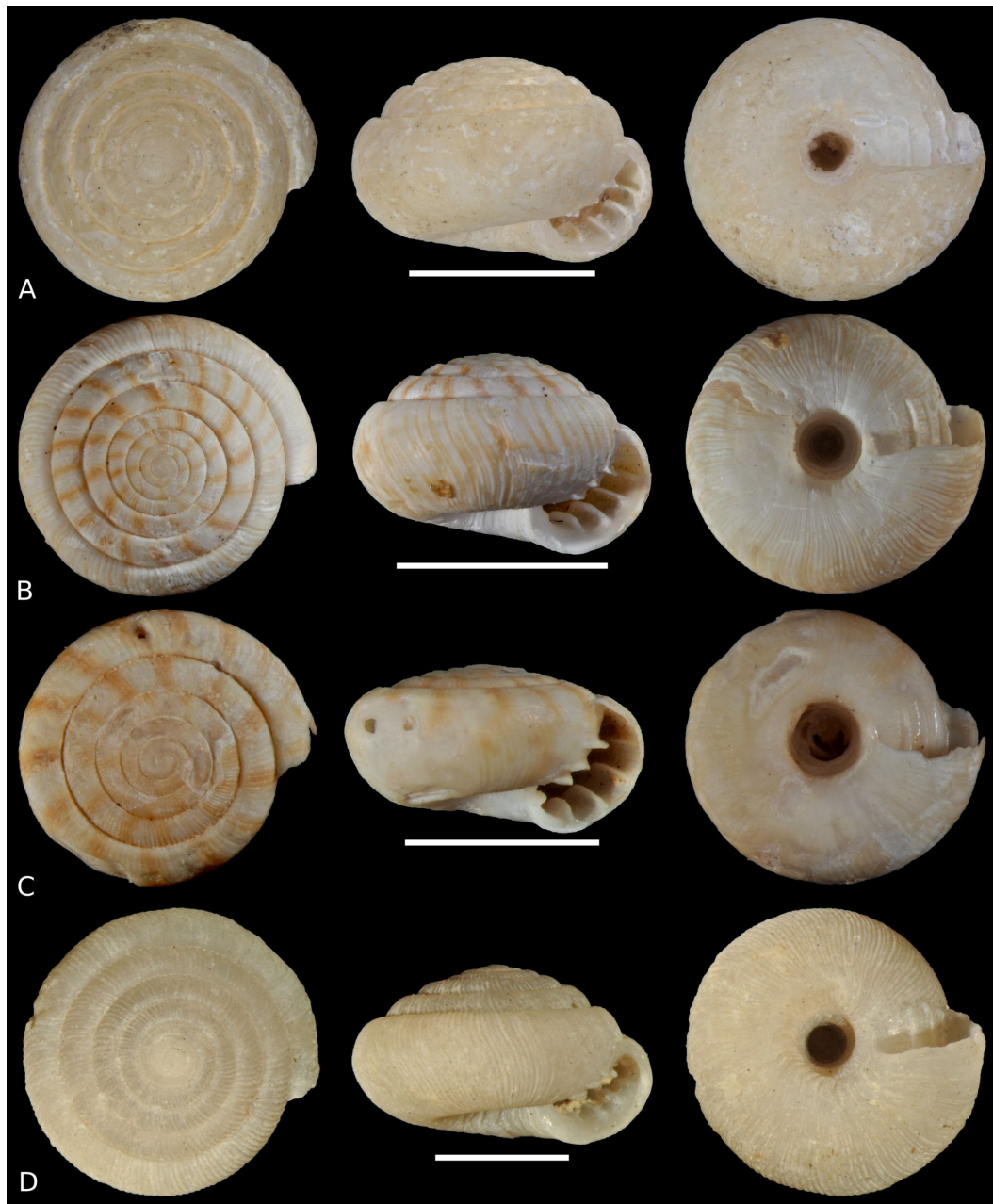


FIGURE 20. A–C. *Kleokyphus hypsus*; A. Holotype (MNHN 25571); B. Specimen 1 (MNHN 25572); C. Specimen 8 (MNHN 25572); D. *Kleokyphus cowiei* sp. nov., holotype (MNHN 25580). Scale bars: A–B = 4 mm; C–D = 2 mm.

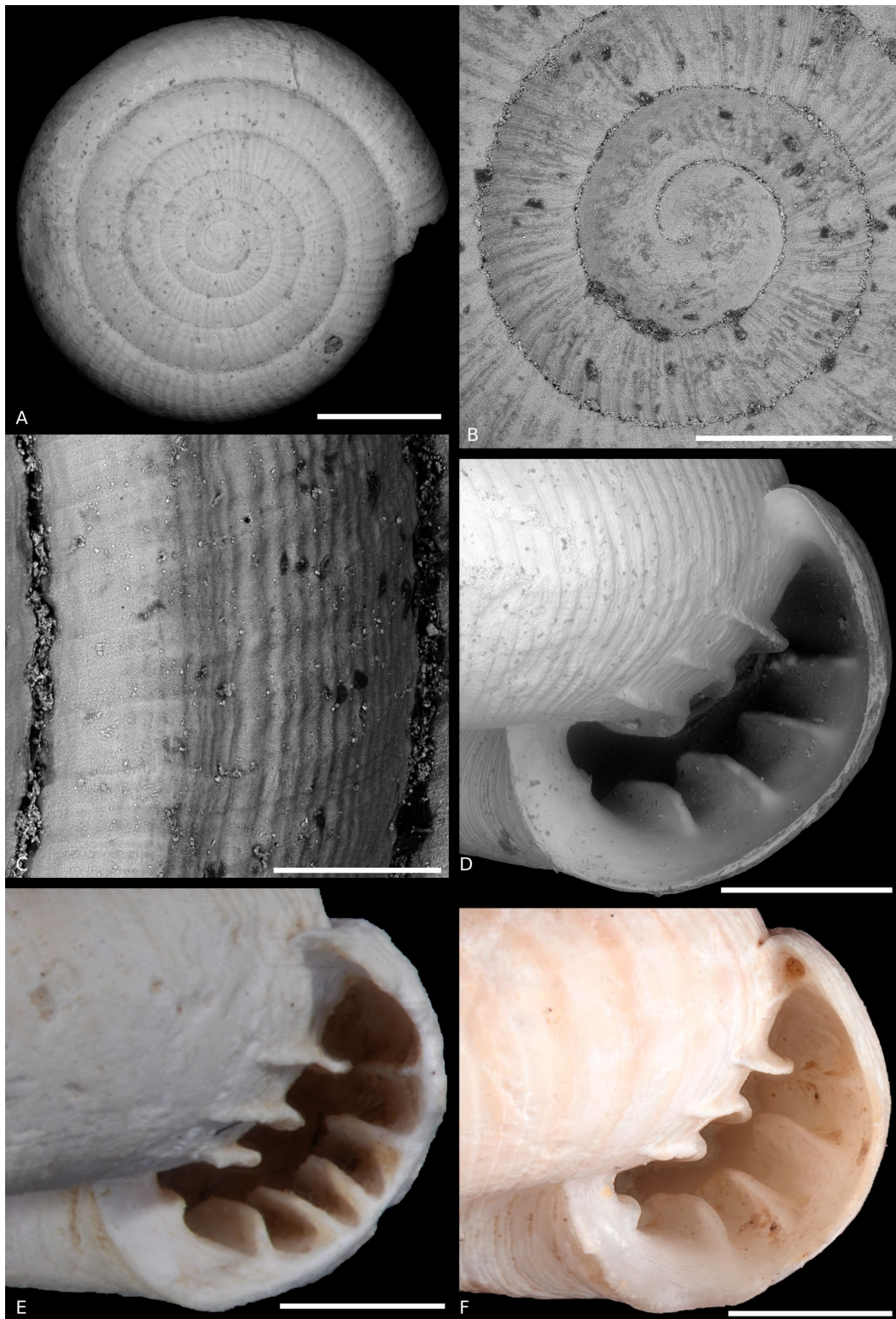


FIGURE 21. *Kleokyphus hypsus*, MNHN 25572. **A.** General view (specimen 10); **B.** Sculpture of the protoconch and early teleoconch (specimen 10); **C.** Sculpture of the late teleoconch (specimen 2); **D.** Detail of the peristome (specimen 1); **E.** Specimen 9, with palatal barrier 3 duplicated; **F.** Specimen 11, with palatal and parietal traces near the apical suture; Scale bars: A,D–F = 1 mm; B = 0.4 mm; C = 0.2 mm.

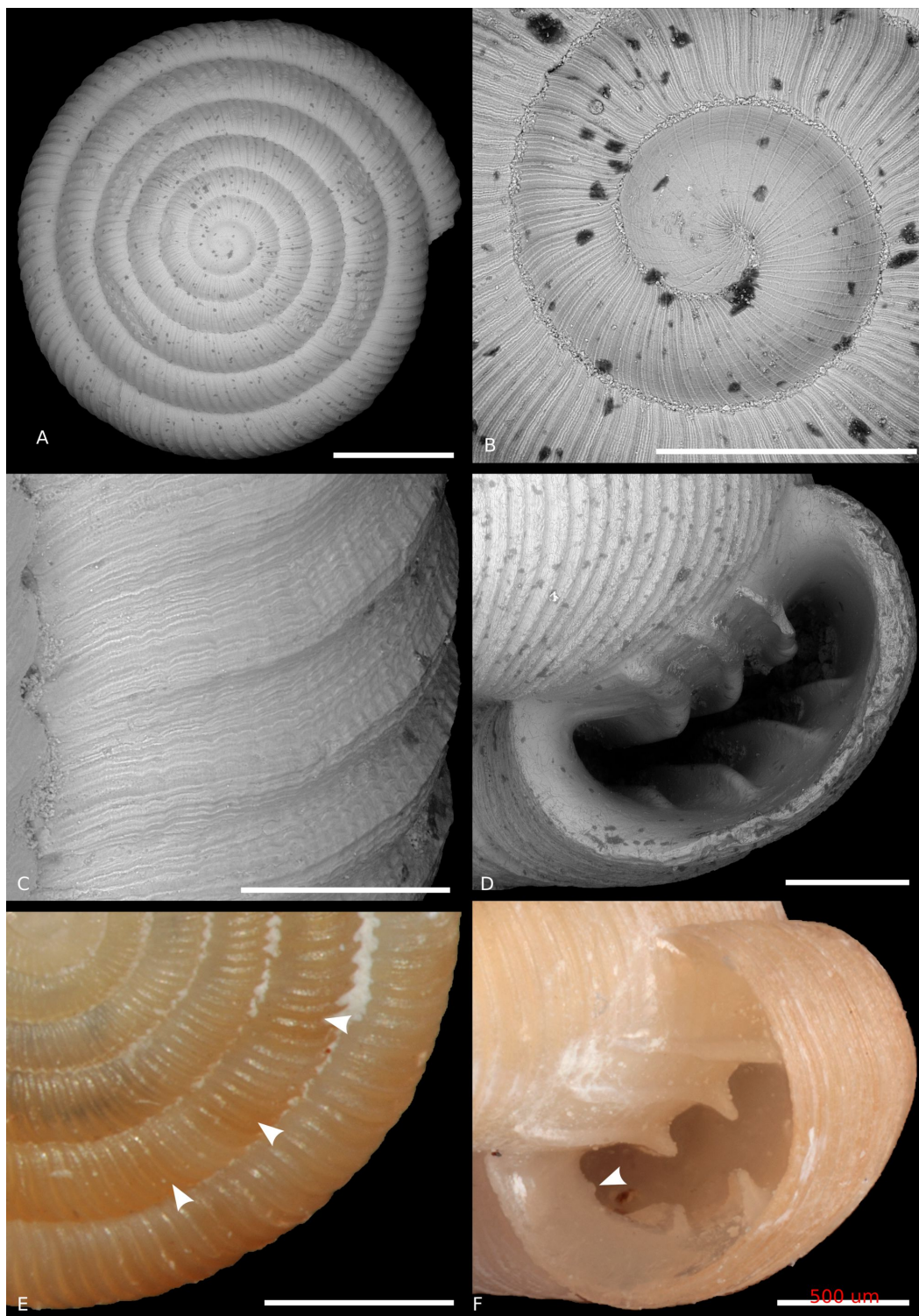


FIGURE 22. *Kleokyphus cowiei* sp. nov. **A–C.** Paratype 1 (MNHN 25581), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Holotype (MNHN 25580), detail of the peristome. **E.** Paratype 3 (MNHN 25581), apical view, showing faint flammulations (arrowheads). **F.** Paratype 5 (MNHN 25581), peristome, showing deeply recessed palatal trace (arrowhead). Scale bars: A,E = 1 mm; B = 0.4 mm; C = 0.2 mm; D,F = 0.5 mm.



FIGURE 23. *Pseudolibera lilliana*. **A.** Holotype (BPBM 115805); **B.** Specimen 1 (MNHN 25589); Scale bars = 5 mm.

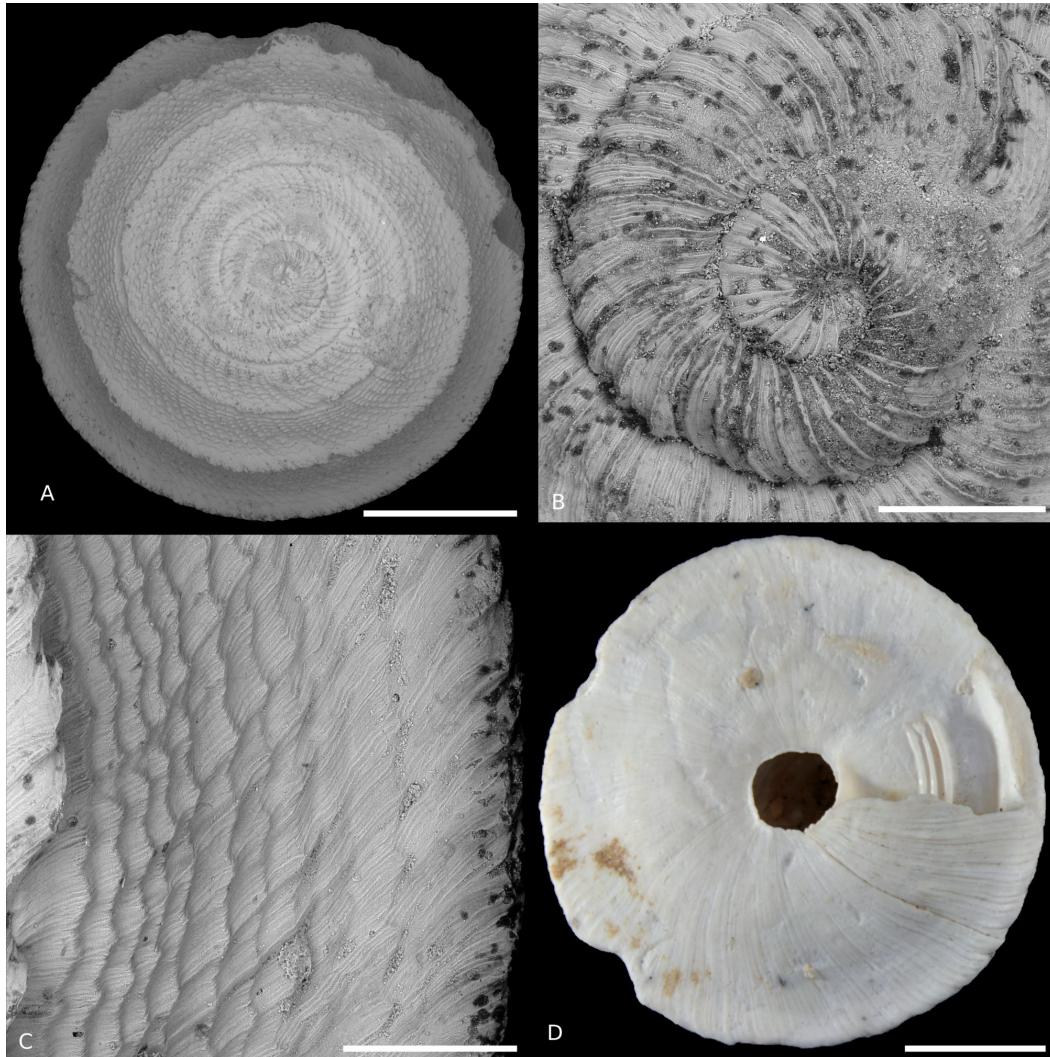


FIGURE 24. *Pseudolibera lillianae* A–C. Specimen 1 (MNHN 25589), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Specimen 9 (station mk16), umbilical view, showing parietal traces flanking the barrier; Scale bars: A,D = 2 mm; B,C = 0.4 mm.

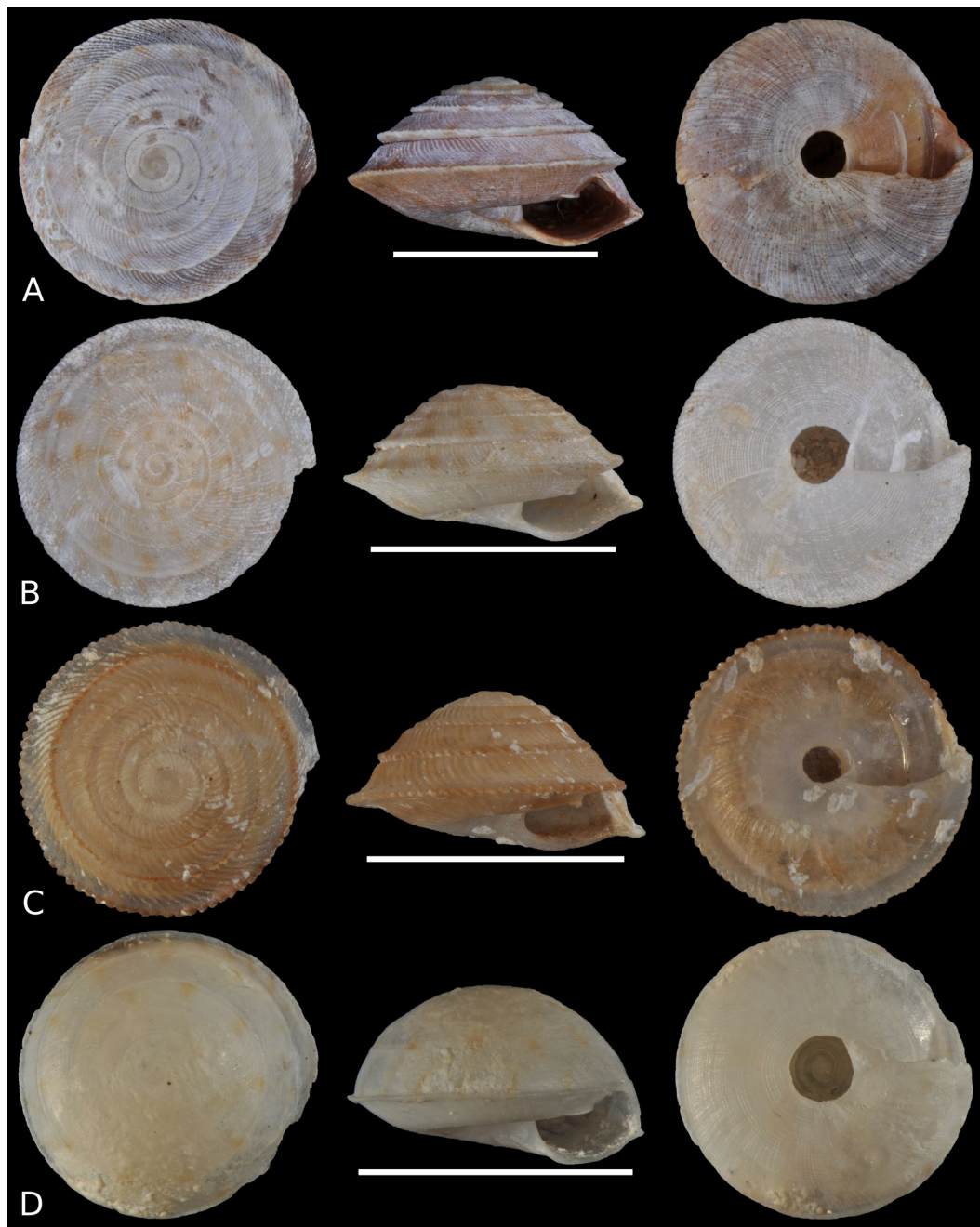


FIGURE 25. Holotypes of: **A.** *Pseudolibera solemi* sp. nov.; **B.** *P. matthiewi* sp. nov.; **C.** *P. cookei* sp. nov.; **D.** *P. aubertdelaruei* sp. nov. Scale bars = 5 mm.

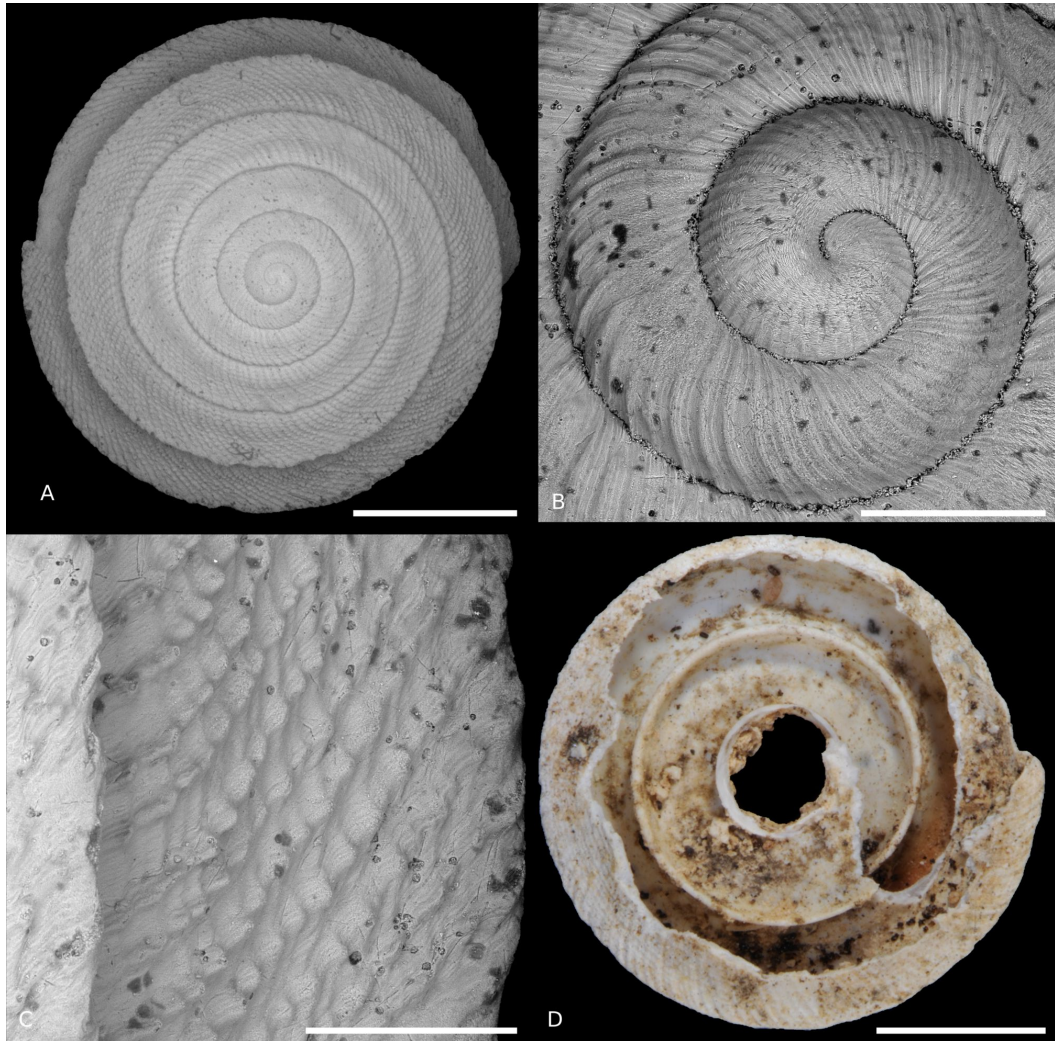


FIGURE 26. *Pseudolibera solemisp.* nov. **A–C.** Holotype (MNHN 25590), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Umbilical view of specimen from station Mk16, showing the apertural barrier extending posteriorly for more than one whorl. Scale bars: A,D = 2 mm; B,C = 0.4 mm.

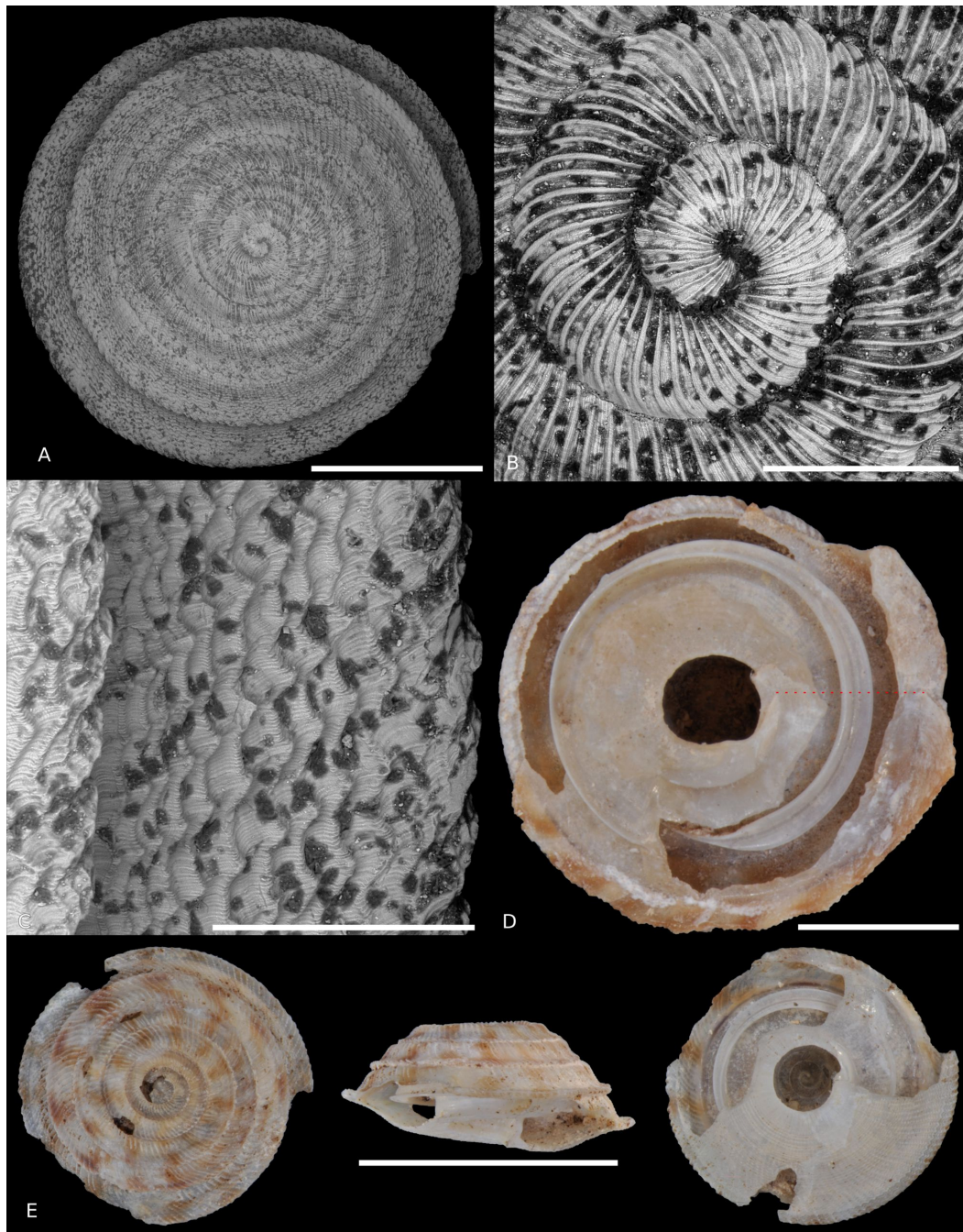


FIGURE 27. *Pseudolibera matthieui* sp. nov. **A–C.** Holotype (MNHN 26531), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Umbilical view of excised specimen (station Mk13), showing the full extent of the bifurcated portion of the parietal barrier; red dashed line indicates the position of the aperture; **E.** Specimen from station Mk19, with the first four whorls of the spire flat; Scale bars: A,D = 2 mm; B,C = 0.4 mm; E = 5 mm.

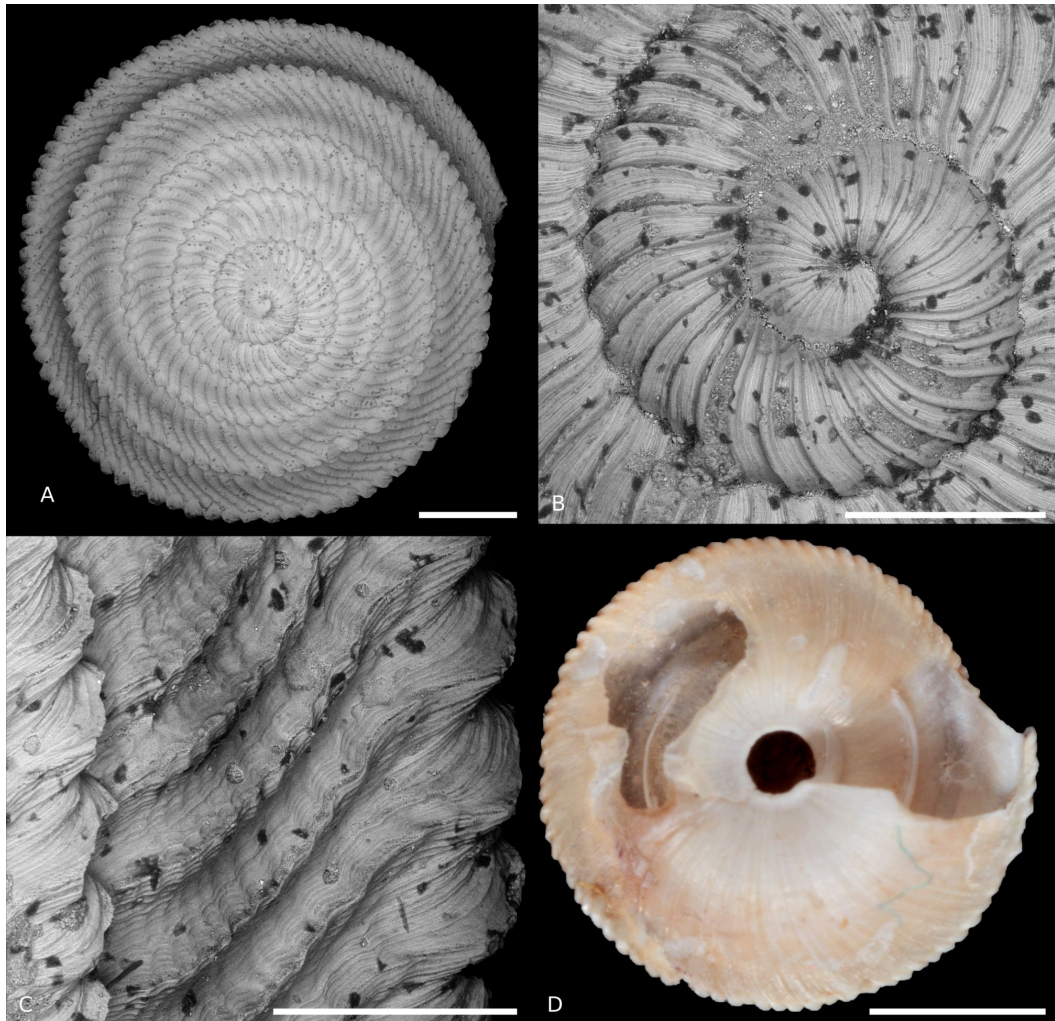


FIGURE 28. *Pseudolibera cookei* sp. nov. **A–C.** Holotype (MNHN 25675), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 4 (MNHN 25676), excised shell base showing the posterior descension of parietal barrier; Scale bars A = 1 mm; B,C = 0.4 mm; D = 2 mm.

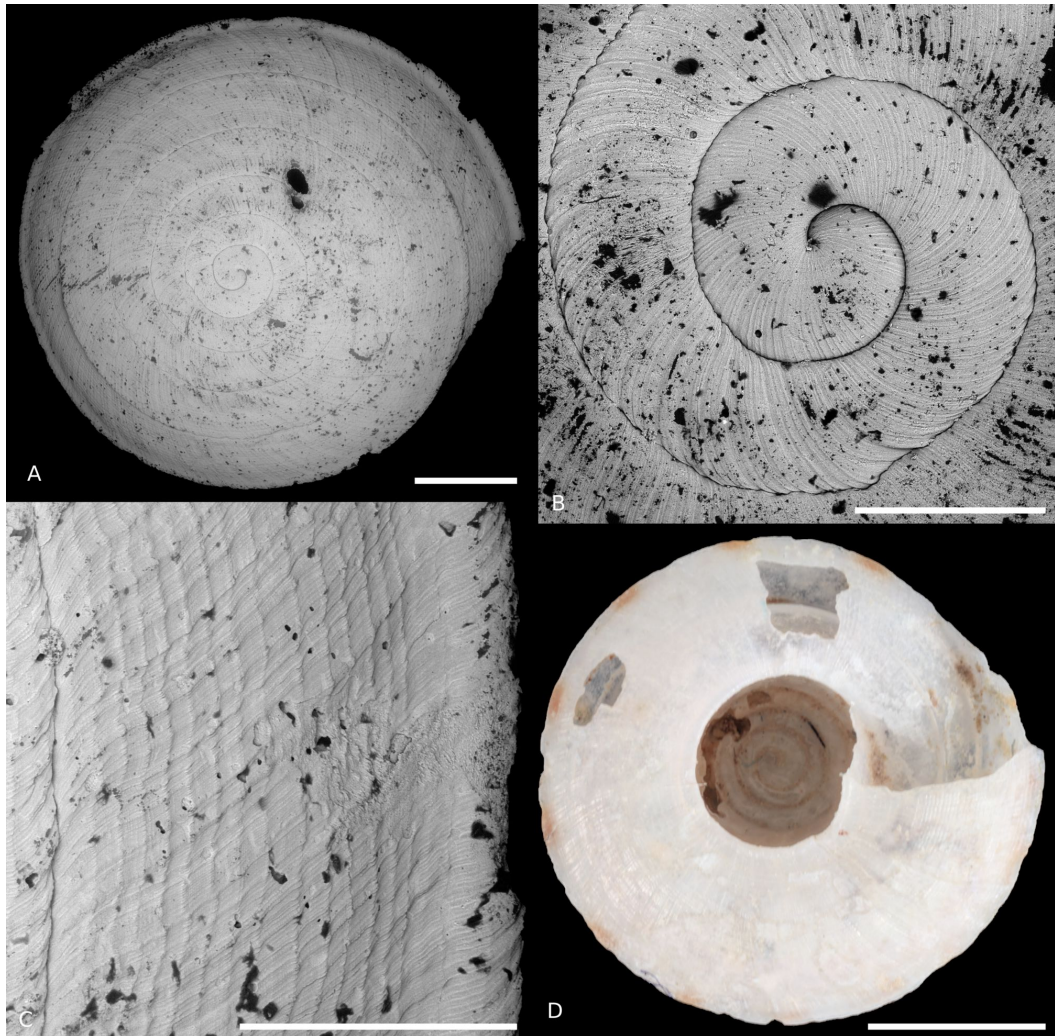


FIGURE 29. *Pseudolibera aubertdelaruei* sp. nov. **A–C.** Paratype 1 (MNHN 25674), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 2 (MNHN 25674), umbilical view, showing portions of the apertural barrier through the damaged shell wall; Scale bars: A = 1 mm; B,C = 0.4 mm; D = 2 mm.

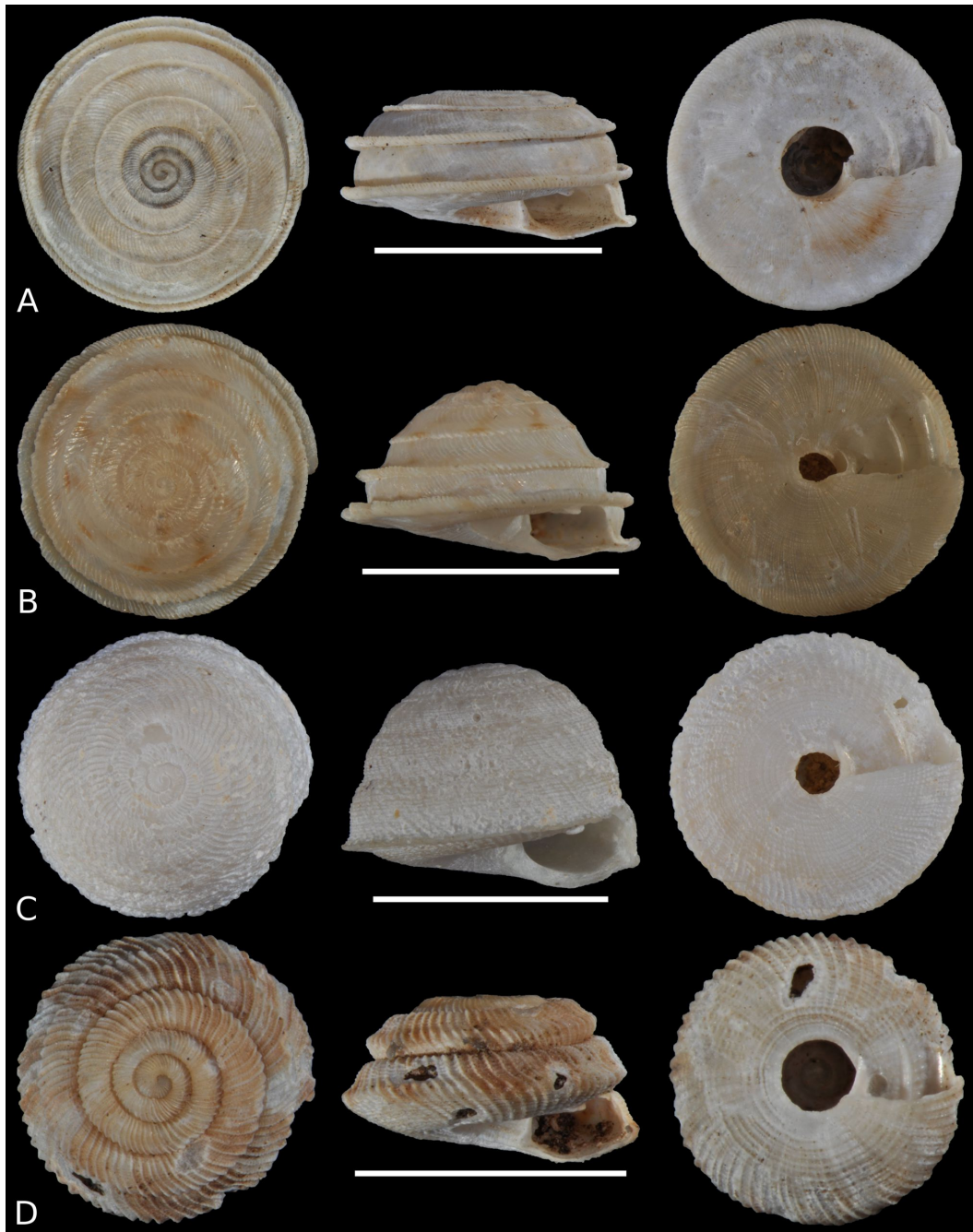


FIGURE 30. Holotypes of: **A.** *Pseudolibera extincta* sp. nov.; **B.** *P. paraminderae* sp. nov.; **C.** *P. elieporoii* sp. nov.; **D.** *P. parva* sp. nov. Scale bars: A–C = 5 mm; D = 3 mm.

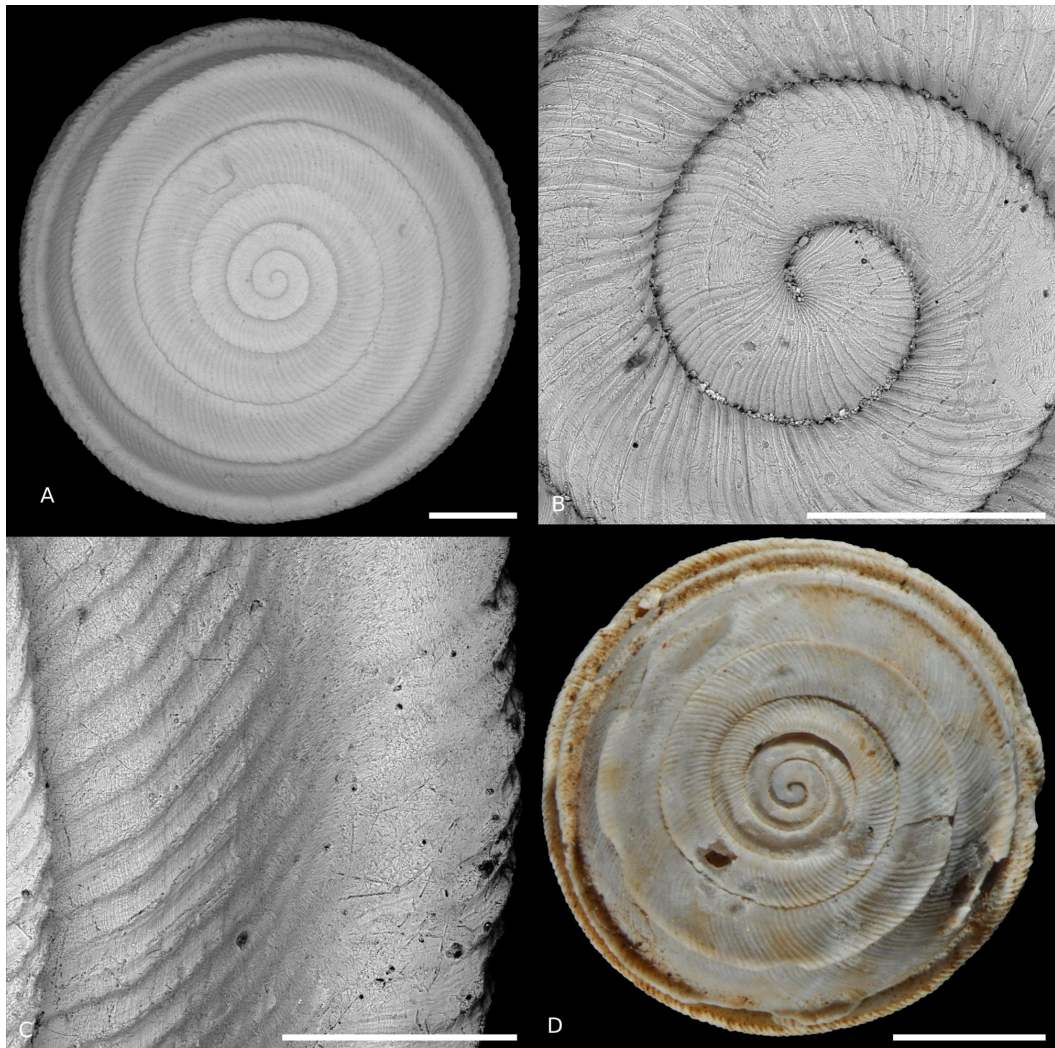


FIGURE 31. *Pseudolibera extincta* sp. nov. **A–C.** Holotype (MNHN 25592), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Paratype 1 (MNHN 25593), showing faint flammulations. Scale bars: A = 1 mm; B,C = 0.4 mm; D = 2 mm.

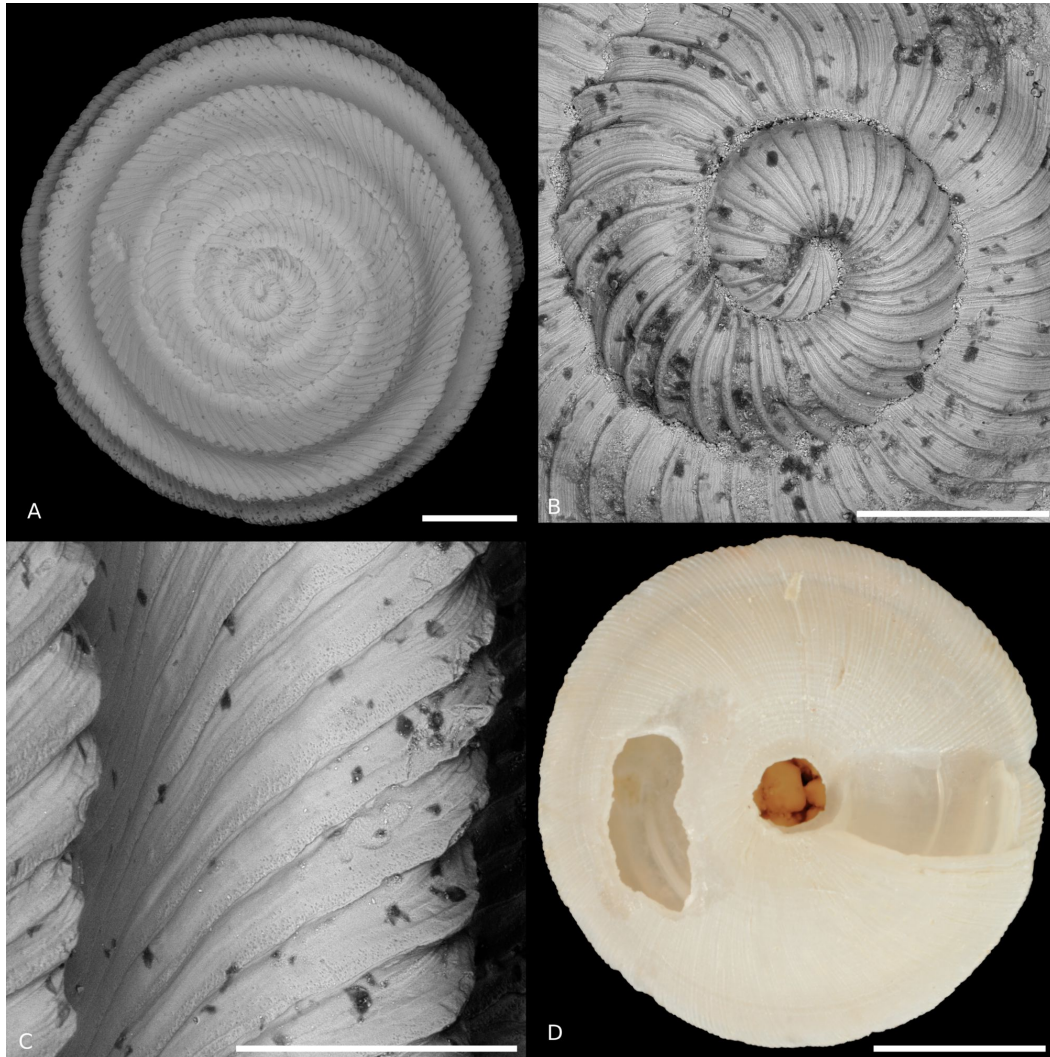


FIGURE 32. *Pseudolibera paraminderæ* sp. nov. **A–C.** Holotype (MNHN 25677), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Ordinary specimen (station Mk04), excised shell base showing the posterior descension of parietal barrier. Scale bars: A = 1 mm; B,C = 0.4 mm; D = 2 mm.

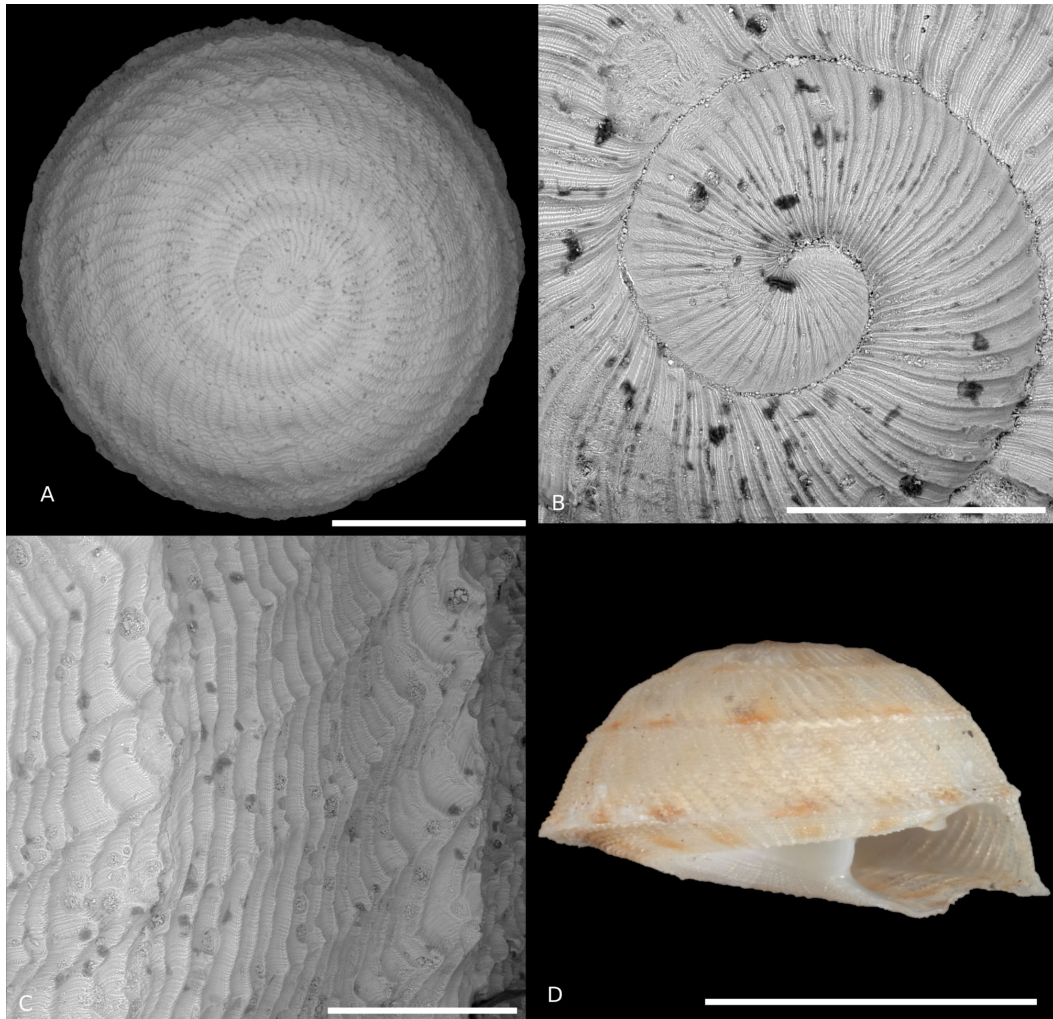


FIGURE 33. *Pseudolibera elieporoi* sp. nov. **A–C.** Paratype 1 (MNHN 25595), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Ordinary specimen showing flammulations. Scale bars: A = 2 mm; B,C = 0.4 mm; D = 4 mm.

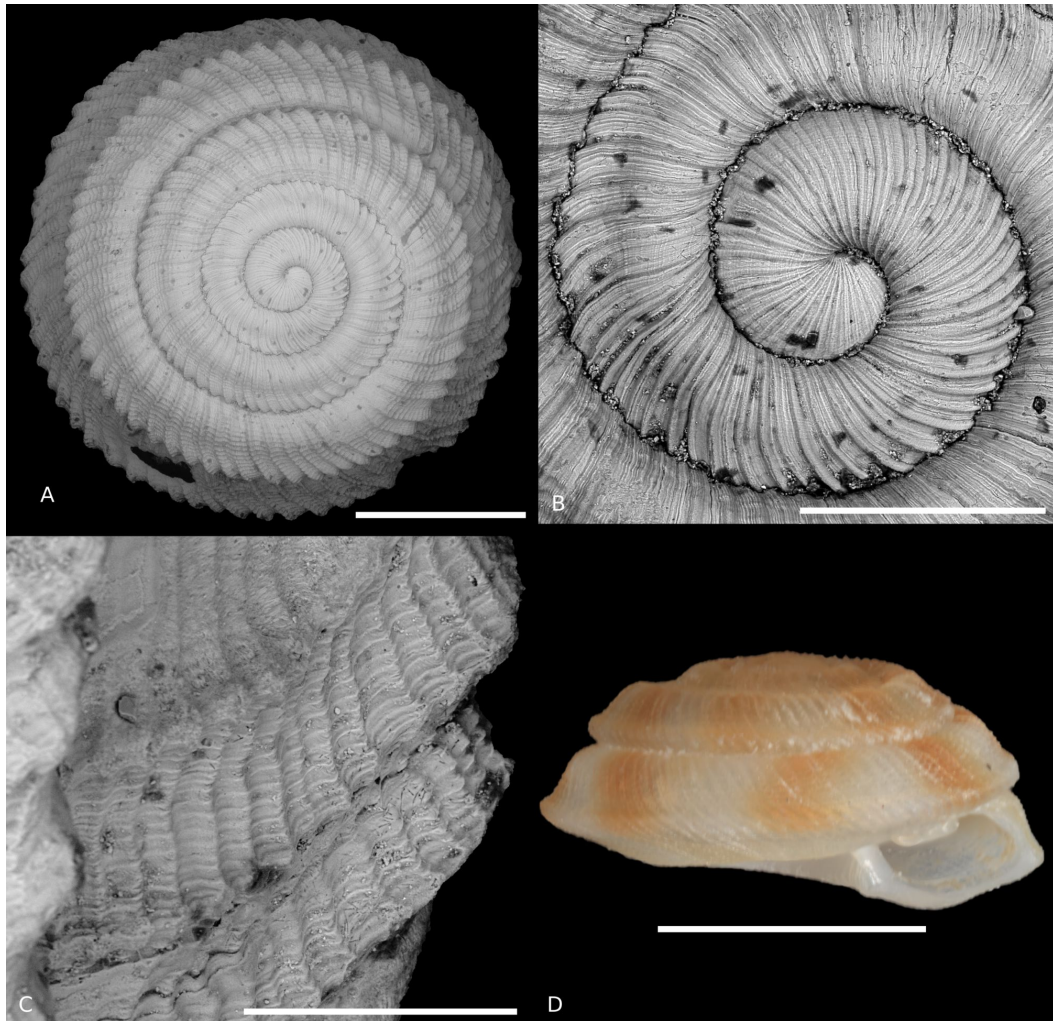


FIGURE 34. *Pseudolibera parva* sp. nov. **A–C.** Holotype (MNHN 25679), apical views; **A.** General view; **B.** Sculpture of the protoconch and early teleoconch; **C.** Sculpture of the late teleoconch; **D.** Ordinary specimen (station Mk12), showing a more tightly coiled spire. Scale bars: A = 1 mm; B = 0.4 mm; C = 0.2 mm; D = 2 mm.



FIGURE 35. Apertural view of the species of *Mautodontha* s.s., *Mautodontha* (*Garrettoconcha*) and *Kleokyphus* of Makatea, illustrated at the same scale: **A.** *M. (M.) daedalea*, ordinary specimen; **B.** *M. (M.) domaneschii* sp. nov., holotype; **C.** *M. (M.) virginiae* sp. nov., holotype; **D.** *M. (G.) occidentalis* sp. nov., holotype; **E.** *M. (M.) harperae* sp. nov., holotype; **F.** *M. (G.) aurora* sp. nov., holotype; **G.** *M. (G.) passosi* sp. nov., holotype; **H.** *M. (G.) temaoensis* sp. nov., holotype; **I.** *M. (G.) spelunca* sp. nov., holotype; **J.** *M. (G.) makateaensis* sp. nov., holotype; **K.** *K. callimus*, paratype; **L.** *K. hypsus*, ordinary specimen; **M.** *K. cowiei* sp. nov., holotype. Scale bar = 3 mm.



FIGURE 36. Apertural view of the species of *Pseudolibera* of Makatea, illustrated at the same scale: **A.** *P. lillianae*, ordinary specimen; **B.** *P. parva* sp. nov., holotype; **C.** *P. paraminderae* sp. nov., holotype; **D.** *P. matthieui* sp. nov., holotype; **E.** *P. aubertdelaruei* sp. nov., holotype; **F.** *P. extincta* sp. nov., holotype; **G.** *P. cookei* sp. nov., holotype; **H.** *P. elieporoii* sp. nov., holotype; **I.** *P. solemi* sp. nov., holotype. Scale bar = 3 mm.

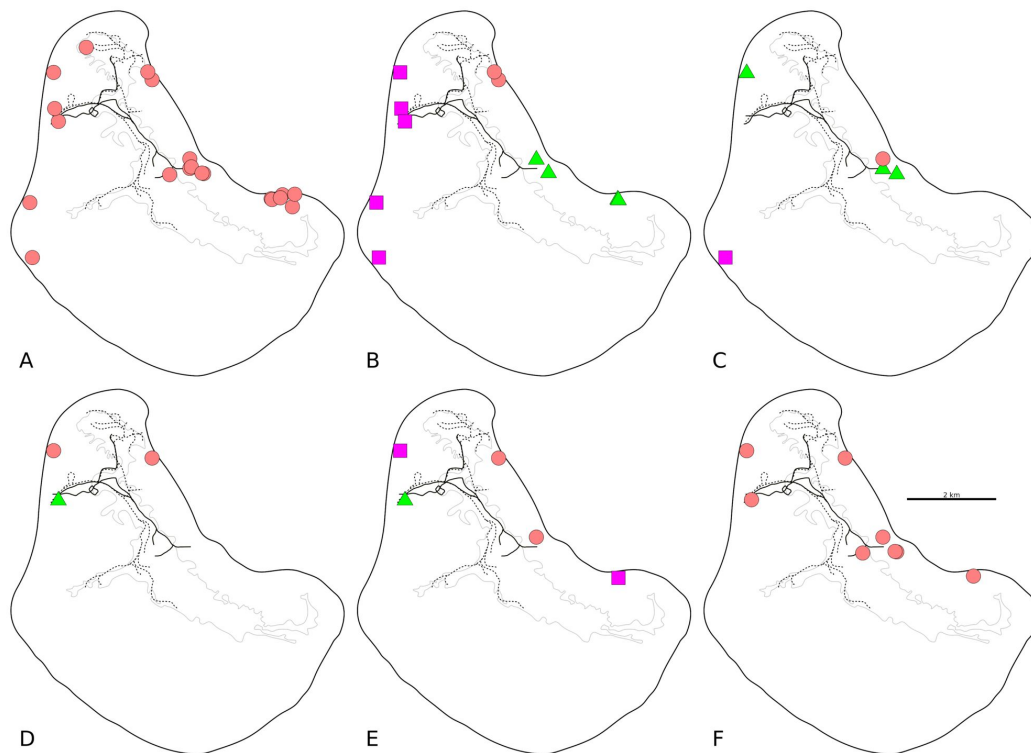


FIGURE 37. Maps of Makatea, showing records of:
A. *Mautodontha*. (*Mautodontha*.) *daedalea*. **B.** circles, *M. (M.) virginiae* sp. nov.; triangles, *M. (M.) domaneschii* sp. nov.; squares, *Mautodontha (Garrettoconcha) occidentalis* sp. nov. **C.** circles, *M. (M.) harperae* sp. nov.; triangles, *Pseudolibera parva* sp. nov.; squares, *M. (G.) spelunca* sp. nov. **D.** circles, *K. hypsus*; triangles, *Kleokyphus callimus*. **E.** circles, *M. (G.) passosi* sp. nov.; triangles, *M. (G.) temaoensis* sp. nov.; squares, *K. cowiei* sp. nov. **F.** *P. lillianae*.

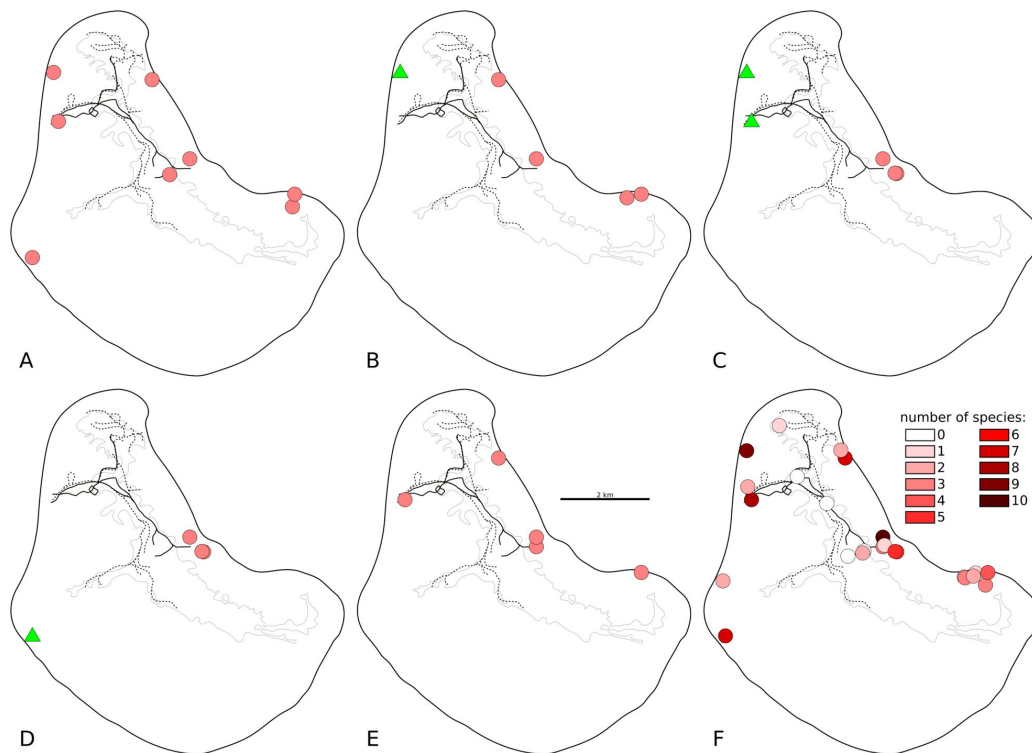


FIGURE 38. Maps of Makatea, showing records of endodontid species (A–D), and a summary of species richness per station (E): **A.** *Pseudolibera solemi* sp. nov. **B.** circles, *M. (G.) aurora* sp. nov.; triangles, *Mautodontha (Garrettoconcha) makateaensis* sp. nov. **C.** circles, *P. paraminderæ* sp. nov.; triangles, *P. extincta* sp. nov. **D.** circles, *P. elieporoii* sp. nov.; triangles, *P. cookei* sp. nov. **E.** *P. matthieui* sp. nov. **F.** species richness indicated by gradient of color from white (zero endodontid species) to very dark red (ten endodontid species)

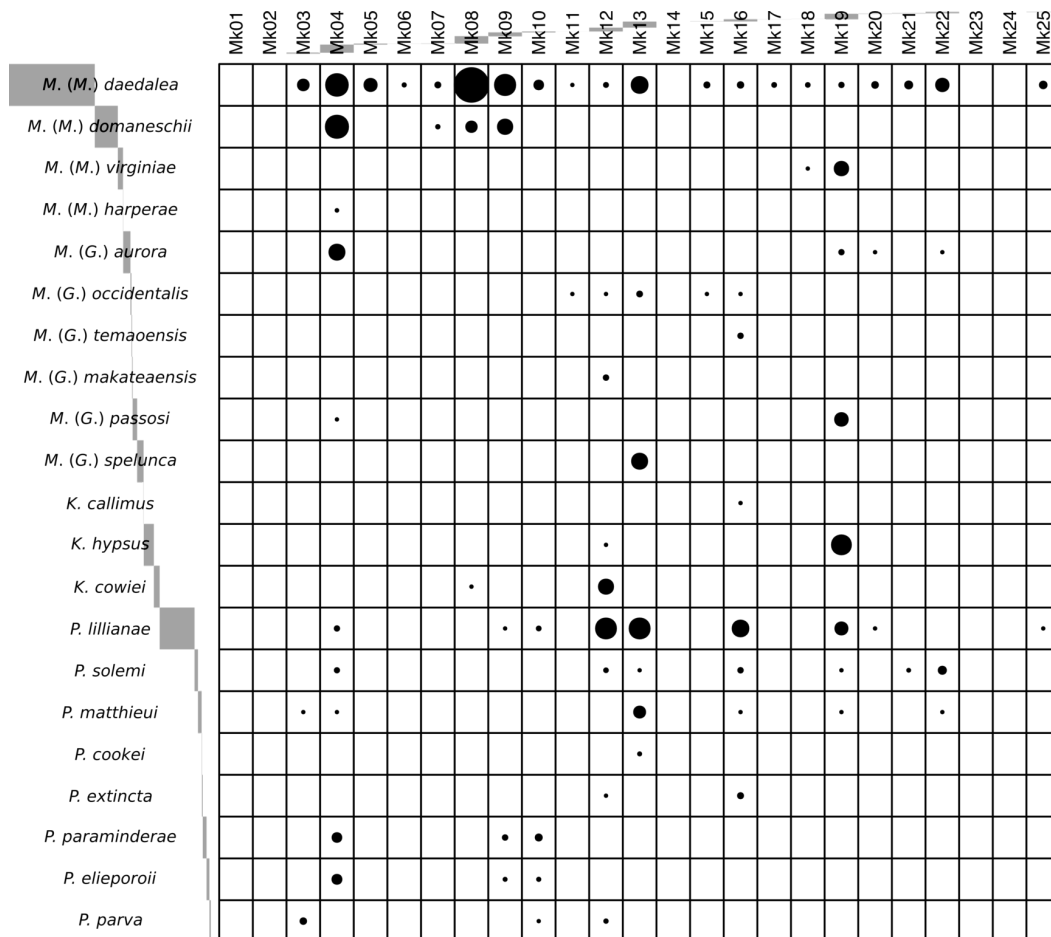


FIGURE 39. Diagrammatic representation of the abundance per station and per species of the endodontid specimens collected in Makatea. The thickness of the bars along the axes and the area of the circles in the grid is proportional to the number of collected specimens.