

BEYOND THE ALIEN INVASION: A RECENTLY DISCOVERED RADIATION OF NESOPUPINAE (GASTROPODA: PULMONATA: VERTIGINIDAE) FROM THE SUMMITS OF TAHITI (SOCIETY ISLANDS, FRENCH POLYNESIA)

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Abstract On Tahiti, invasive species such as the carnivorous snail *Euglandina rosea* or the tree *Miconia calvenscens* have impacted much of indigenous species or habitats, even in remote places not affected by agriculture or development. However, thanks to the extreme ecological conditions in altitude, these invasive species have not reached higher elevation where patches of native vegetation with endemic flora and fauna still occur. On Mount Aorai, second highest peak of Tahiti (2066 m), the impact of *Euglandina rosea* and *Miconia calvenscens* reach a maximum altitude of 1400 m. Above this altitude, endemic gastropod species are still found alive and some remain undescribed. A new genus of Vertiginidae, *Nesoropupa* n. gn., is described for four new species from the top 500 m of Mount Aorai and Mount Marau: *N. duodecim* n. sp. (type species), *N. fenua* n. sp., *N. nathaliae* n. sp. and *N. fontainei* n. sp. Also discussed is how the impact of global warming is allowing introduced species to colonize higher altitudes up to the summits.

Key words *Nesoropupa* n. gn., new species, Tahiti, altitudinal ceiling, global warming.

INTRODUCTION

Situated 17.5°S and 149.5°W in the South Central Pacific Ocean, Tahiti is part of the Society Islands archipelago (French Polynesia) of which it is the youngest (except the small islet of Mehetia). It is entirely volcanic and its oldest ground has been dated 1.4 My (Clouard & Bonneville, 2004). With an overall area of 1042 sq. km and reaching 2241 m at Mt Orohena, it is by far the largest and highest island of French Polynesia. It is also the most populated island with 69% of the total population and a density of 145 inhabitants per sq. km (Frouté, 1997).

Since the 1980s, the land snail fauna of the Society Islands, in particular that of Tahiti, has received much attention through the dramatic story of the introduction of *Euglandina rosea*, which has driven to extinction dozens of partulid snail species (Clarke, Murray & Johnson, 1984; Coote & Loeve, 2003; Coote, Loeve, Meyer & Clarke, 1999; Cowie, 1992; Murray, Murray, Johnson & Clarke, 1988; Pearce-Kelly, Clarke & Mace, 1994; Tillier & Clarke, 1983). Since the last description of a land snail species from Tahiti published in 1983 (Solem, 1983), most, if not all published studies on terrestrial mollusks in French Polynesia were those documenting these extinctions. Similarly, the recent invasion by the South American tree *Miconia calvenscens* has destroyed most of the remaining natural

forests which had escaped deforestation, fires or other degradations (Meyer & Florence, 1996), highlighting once more the biodiversity crisis on Tahiti. However, recent field work on Mount Aorai, the second summit of Tahiti (2066 m), has shown that neither *E. rosea* nor *M. calvenscens* have reached the summit (Coote *et al.*, 1999; Meyer & Florence, 1996) where well preserved patches of natural forest still harbor a rich endemic fauna of various, sometimes undescribed, groups (i.e. Hoch, 2006).

The last comprehensive list of land snails of the Society Islands (Garrett, 1884) is more than 120 years old. Later, some groups received more attention with global revision of the Pacific region: Achatinellidae / Tornatellinidae (Cooke & Kondo, 1960), Euconulidae (Baker, 1938; 1941), Punctidae, Charopidae and Endodontidae (Solem, 1976; 1983). Based on this literature, a rough estimate recognized about 100 indigenous species on Tahiti, of which about half are strictly endemic to the island. Nevertheless, the exact number of land snail species on Tahiti remains unknown.

The Vertiginidae are widely distributed around the world (except Antarctica) and can be found in all types of habitats, from cold to tropical environments (Pilsbry, 1920-1921; Pilsbry & Cooke, 1918-1920; Schileyko, 1998). The species found in the Pacific Islands all belong to Nesopupinae Steenberg, 1925, a subfamily inhabiting all tropical and subtropical regions of the world. Despite

	<i>Indopupa</i>	<i>Afripupa</i>	<i>Helenopupa</i>	<i>Cocopupa</i>	<i>Nesopupilla</i>	<i>Nesopupa</i>	<i>Nesodagys</i>	<i>Insulipupa</i>	<i>Infranesopupa</i>	<i>Limbatipupa</i>	<i>Pronesopupa</i>	<i>Edentulopupa</i>	<i>Sericipupa</i>	<i>Nesoropupa</i>
Angular lamella Curved (0) Strait (1) Short (2) Not present (3)	0	0	0	0	0	0	0	1	2	2	3	3	3	3
Columellar lamella Strait (0) Curved (1) Not present (?)	0	0	0	0	1	1	0	0	0	0	?	?	?	0
Pitted sculpture on teleoconch Present (0) Lost (1)	0	1	1	0	0	0	0	0	0	1	1	1	1	1
Spiral sculpture on the protoconch Absent (0) Present (1) only some species (?)	0	0	0	0	0	?	0	0	0	0	0	1	0	1
Radial striation on teleoconch Present (0) Dense (1) Lost (2)	0	1	2	2	1	0	0	2	2	0	0	0	1	1
Periostracal edge on radial ribs Present (0) Lost (1)	0	1	1	1	1	1	0	1	1	0	0	0	1	1
Basal apertural lamellae Present (0) Lost (1) depending the species (?)	0	0	0	0	0	0	0	0	0	0	1	1	1	?
Relative aperture size Small (0) Large (1)	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Aperture Rounded (0) Rhomboid (1)	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Table 1 Comparison of selected characters and their states in some Nesopupinae.

their minute size, species of Nesopupinae from French Polynesia were first described as early as 1847 (*Pupa tantilla* Gould, 1847). After a brief overview by Boettger (1880) illustrating a set of scattered single island endemic species, Pilsbry and Cooke (Pilsbry, 1920-1921; Pilsbry & Cooke, 1918-1920) arranged the currently used taxonomy of these Polynesian Nesopupinae (see Schileyko, 1998). They described a dozen new "sections" in order to reflect the various lineages. Since then, only the *Lyropupa* radiation in Hawaii has received attention (Pokryszko, 1997). However, Nesopupinae (especially *Nesopupa* species) are likely to occur throughout the whole Pacific Ocean islands (Solem, 1959; Preece, 1995), thus our gap in knowledge is immense: we are just in the first steps of understanding Pacific Vertiginidae.

Presented in this paper are the descriptions of four new species of Nesopupinae recently discovered from the summits of Mount Aorai and Mount Marau on Tahiti. These species clearly show a common set of characters differing from all other Nesopupinae, suggesting a common ancestor and history. Thus, a new genus, *Nesoropupa*, is erected in order to reflect this radiation.

ABBREVIATIONS

- ANSP Academy of Natural Sciences of Philadelphia, USA.
 BPBM Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
 MCZ Museum of Comparative Zoology, Cambridge, USA.
 MNHN Muséum national d'Histoire naturelle, Paris, France.
 NMBE Natural History Museum, Bern, Switzerland.
 SMF Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany.

In the lists of examined material, *sh* refers to complete dead shells, *fg* to fragments, *ju* to juveniles.

MATERIAL AND METHODS

The material herein described derives from three days of collecting on Mt Marau (13 November 2002) and Mt Aorai (15-16 November 2002), Tahiti, French Polynesia, by Benoît Fontaine and the author (Appendix 1). Shells were collected by

hand-picking and by sieving of the litter on the ground. Alive individuals were photographed.

In addition to the material described here, many taxa of Nesopupinae from the Pacific region have been examined for comparison, listed in the Appendix 2. Many lots of *Nesopupa* and *Pronesopupa* from the Austral Islands, Tahiti and Makatea that were collected between 2002 and 2004 by Benoît Fontaine and the author were also examined. All the material collected during this field work is deposited in the MNHN.

In order to compare the new genus with other described Nesopupinae genera, a character matrix (Table 1) was elaborated based on Pilsbry and Cooke conchological descriptions (Pilsbry, 1920-1921; Pilsbry & Cooke, 1918-1920). Listed are those characters and their states that are constant within a genus but variable among genera.

Potential area of occupancy (see "Conservation issues" in the discussion) was calculated under a Geographic Information System with georeferenced maps issued from Dupon (1993: Pl. 7) and Florence (1993).

SYSTEMATIC DESCRIPTIONS

SUPERFAMILY PUPILLOIDEA Turton, 1831
 FAMILY VERTIGINIDAE Fitzinger, 1833
 SUBFAMILY NESOPUPINAE Steenberg, 1925

Genus *Nesoropupa* n. gn.

Type species *Nesoropupa duodecim* n. sp.

Description Shell small (less than 4mm in height), dextral or sinistral, oval to cylindrical, thin and fragile, almost translucent and only lightly calcified. Color brown corneous, becoming pale brown after wearing on the ground. Protoconch always less than two whorls, finely striated with microscopic discontinuous spiral grooves. Transition protoconch/teleoconch rather visible due to the difference in microsculpture. Surface of postapical whorls rather brilliant, with delicate, radial, oblique, crowded, regularly spaced riblets. Whorls slightly convex to almost flat, with most convexity below the middle and sometimes with an angular hump overhanging the suture and delimiting a basal crest. Aperture rhomboidal to piriform, often angulated on the infrapalatal wall, prosocline, with

weakly reflexed margins and thin parietal callus. Angular lamella absent or, rarely, vestigial and then on parietal wall rather than in aperture angle. Other lamellae, one to four in number, rather thick and short, none of them reaching the aperture edge and in most cases visible in frontal view: one straight parietal lamella, sometimes absent, in the middle of the parietal wall, being less deeply situated inside the aperture than other lamellae; columellar lamella present in all four known species, sometimes almost invisible in frontal view, subhorizontal, not bent downward and going regularly upward over ca. one quarter of whorl; zero, one or two palatal lamellae sometimes reduced to tubercle, visible in frontal view and generally also from the exterior due to shell transparency. Interior of the shell (lamellae included) covered by more or less dense, minute (less than 3µm) scales, with the free end oriented toward the aperture. Umbilicus tiny.

Anterior superior part of the body black, the rest (posterior part, foot) white. Head lacking the two lower tentacles (Figure 8).

Habitat and distribution The genus *Nesoropupa* is only known from Mt Aorai and Mt Marau on Tahiti (Society Islands, French Polynesia). It is present above ca. 1400 m only, where native scrub mountainous vegetation dominated by a *Metrosideros collina*-*Weinmannia parviflora* dwarf (2-3m in height) forest, with *Ilex anomala*, *Myrsine* spp. and *Vaccinium cereum* var. *cereum* (Florence, 1993; Meyer, in press). Living specimens have been observed on leaves of *Astelia nadeaudii*, a plant characteristic of the summit shrublands and endemic to the highest Society Islands (Tahiti, Moorea and Raiatea). They have an arboreal way of life, but it is possible that some species are ground-dwelling.

Derivation of name From the Greek *neso-*, island, *-oro-*, mountain and the Latin *-pupa*, doll, this latter commonly used for pupilloid snails regarding the resemblance with swaddling clothes of dolls. Gender: feminine.

Remarks Diagnostic characters of the genus *Nesoropupa* are the rhomboidal to piriform shape of the aperture and the sub-middle convexity of the whorls (these two characters being linked) as well as the combination of the following characters: lack of angular lamella, protoconch microsculpture of fine discontinuous spiral grooves

	Shell height	Shell width	Shell height/ width ratio	Aperture height	Aperture width
<i>Nesoropupa duodecim</i> (n=26)					
holotype	1.82	1.16	1.57	0.64	0.7
range	1.72-2.16	1.1-1.24	1.48-1.8	0.62-0.8	0.64-0.78
mean	1.93	1.17	1.65	0.7	0.7
sd	0.12	0.04	0.09	0.05	0.04
<i>Nesoropupa fenua</i> (n=3)					
holotype	3.24	1.36	2.38	0.9	0.84
range	3.16-3.46	1.28-1.56	2.03-2.7	0.9-0.92	0.72-0.84
mean	3.29	1.4	2.37	0.91	0.78
sd	0.16	0.14	0.34	0.01	0.06
<i>Nesoropupa nathaliae</i> (n=20)					
holotype	2.7	1.24	2.18	0.8	0.72
range	2.1-2.8	1.14-1.26	1.8-2.34	0.72-0.86	0.68-0.8
mean	2.63	1.21	2.18	0.81	0.74
sd	0.22	0.03	0.16	0.03	0.04
<i>Nesoropupa fontainei</i> (n=14)					
holotype	3.36	1.64	2.05	1.06	0.96
range	3.14-3.64	1.52-1.72	1.91-2.29	0.88-1.06	0.84-0.96
mean	3.42	1.6	2.13	0.96	0.89
sd	0.12	0.06	0.12	0.05	0.03

Table 2 Dimensions (in mm) and proportions of the four new species of *Nesoropupa*. sd=standard deviation

and not hammered or pitted, regular sculpture of radial striae without periostracal edge, inner end of columellar lamella straight or slightly upturned, aperture margin not or only slightly expanded and fragility of the shell.

The latter character is a result of light calcification, while the periostracum remains quite resistant. More than half of the shells collected are broken, but often only the periostracum remains without the calcareous layer. The only other Nesopupinae on Tahiti, which belong to *Nesopupa*, have a much stronger shell.

Variations between *Nesoropupa* species are the dextral or sinistral coiling, shell size and shape, number and development of apertural barriers. All four species are easily distinguishable from each other, with no intermediate form observed. They are all found in syntopy (summit of Mt Aorai).

Key to genus *Nesoropupa*

1. shell dextral 2
- shell sinistral 3
2. four apertural lamellae *N. duodecim*
- only one (columellar) lamella *N. fenua*
3. three apertural lamellae (sometimes four), shell subcylindrical *N. nathaliae*
- two apertural lamellae, shell ovate to globose *N. fontainei*

Nesoropupa duodecim n. sp.

Fig. 1A, 2B, 3C-D, 4A, 4E, 5C-D and 7

Type material Holotype (MNHN 9934), three paratypes (MNHN 9935) and two paratypes (BPBM 282927).

Type locality Summit of Mt Aorai, alt. 2065 m, Tahiti, 17.61317°S, 149.4952°W.

Material examined A total of 61 specimens. Mt Marau, 1430 m, 2 sh, 8 jv/fg; Mt Aorai, 1520 m, 1 sh; Mt Aorai, 1725 m, 1 sh and 1 jv/fg; Summit of Mt Aorai, 2065 m, 32 sh (holotype and all paratypes), 16 jv/fg.

Diagnosis A small dextral species of *Nesoropupa*, oval shaped, with four lamellae: one parietal, one columellar, one lower palatal and one upper palatal.

Description (Holotype) Shell very small (height 1.82mm), dextral, oval to subcylindrical, thin and fragile, almost translucent. Color light brown corneous. 4.75 whorls. Protoconch of about 1.5 whorls finely striated with microscopic discontinuous spiral grooves. Transition protoconch/teleoconch only slightly visible.

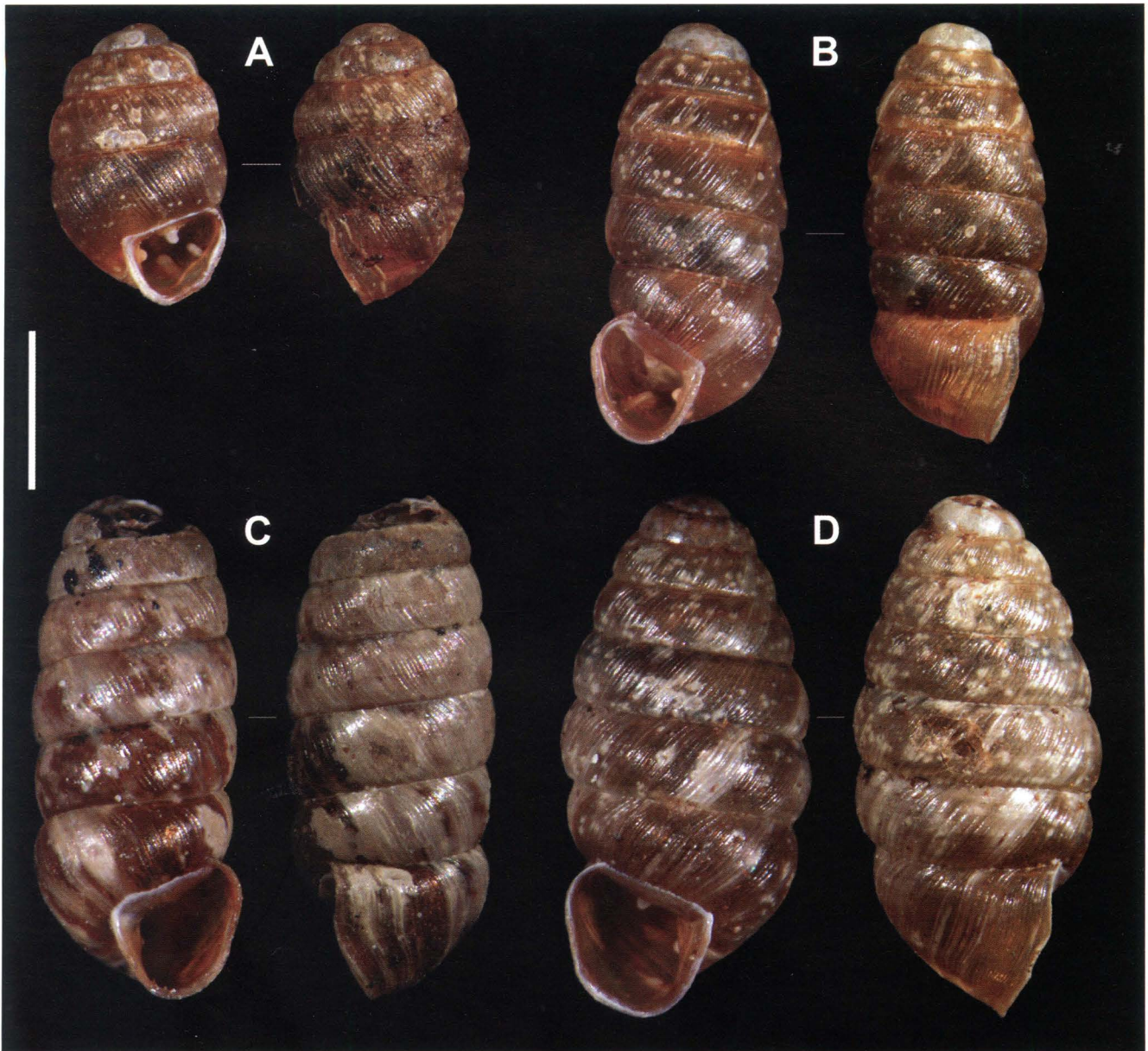


Figure 1 Holotypes. **A** *Nesoropupa duodecim* n. sp., **B** *N. nathaliae* n. sp., **C** *N. fenua* n. sp., **D** *N. fontainei* n. sp. Scale bar = 1mm.

Surface of postapical whorls rather brilliant, with delicate, radial, oblique, crowded, regularly spaced riblets, ca. 28 per mm on the last whorl. Whorls slightly convex with most convexity below the middle. Aperture sub-rhomboidal, angulated on the infrapalatal wall, prosocline, with weakly reflexed margins and thin parietal callus. Angular lamella absent or, rarely, vestigial and then on parietal wall rather than in aperture angle. Four rather thick and short lamellae, none of them reaching the aperture edge and all visible in frontal view: one straight parietal lamella in the middle of the

parietal wall and perpendicular to it, being less deeply situated inside the aperture than other lamellae; columellar lamella subhorizontal going regularly upward over ca. one quarter of whorl; two palatal lamellae, the lower one more developed than the upper one, visible from the exterior by transparency. Interior of the shell (lamellae included) covered by dense, minute (less than $3\mu\text{m}$) scales with the free end oriented toward the aperture. Umbilicus tiny.

Measurements Dimensions and proportions of 26 adult specimens: see Table 2 and Figure 9.

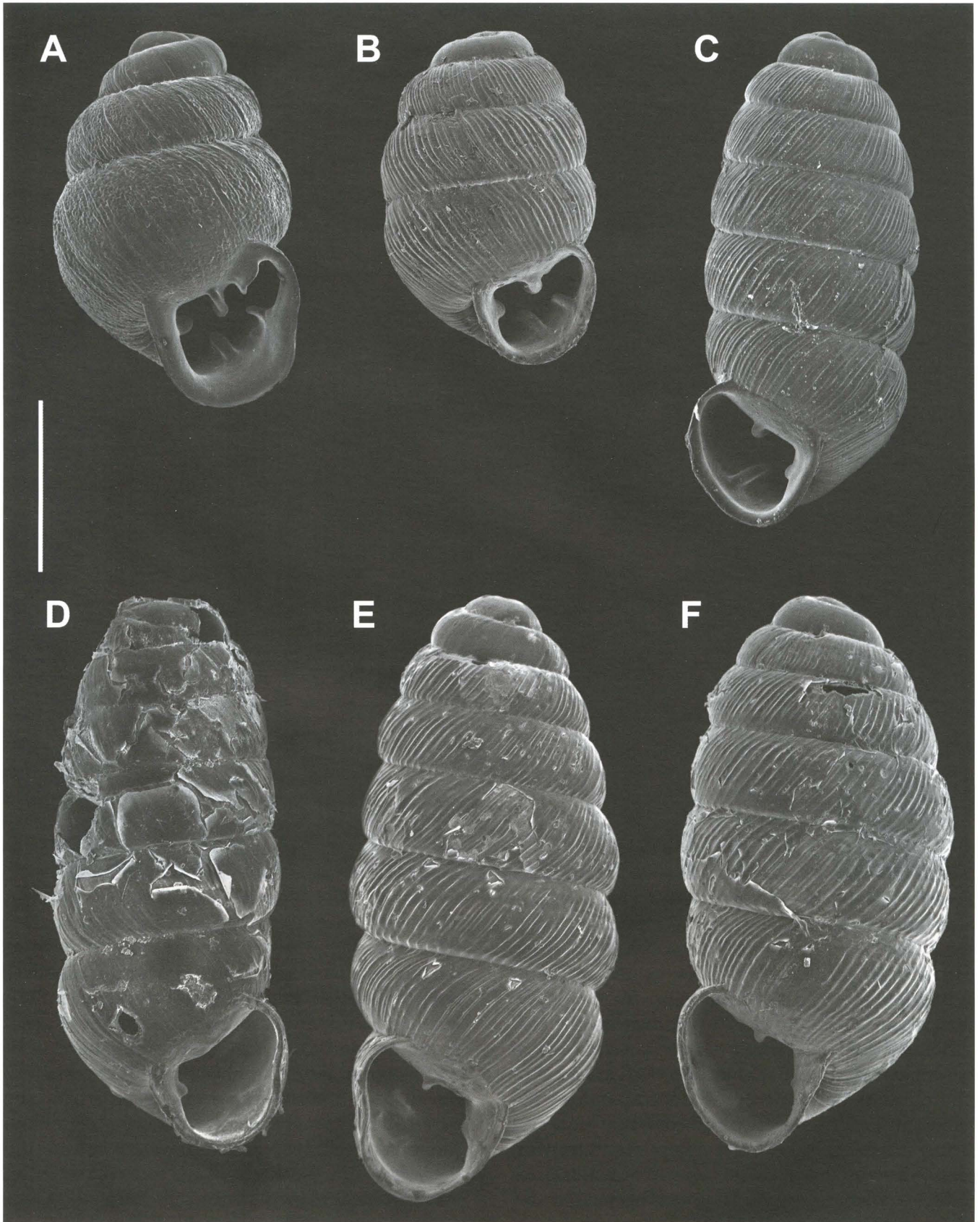


Figure 2 Shells (SEM photographs). All from summit of Mt Aorai (Th16) except A and F. **A** *Nesopupa* sp., 6km inside Papeno'o valley, Topatari waterfall (Th29) **B** *Nesoropupa duodecim* **C** *N. nathaliae* **D** *N. fenua* **E** *N. fontainei* **F** *N. fontainei*, Mt Marau (Th05). Scale bar = 1mm.

Derivation of name From the Latin *duodecim*, twelve; treated as a noun in apposition. It relates to the fact that the species is found above 1200 m elevation.

Proposed common names Summit whorl snail (English), Maillot du haut des cîmes (French).

Habitat and distribution *N. duodecim* is known from Mt Aorai and Mt Marau and should be found on other peaks, at least Mt Orohena. It lives in the *Metrosideros* scrub mountainous vegetation, not below 1430 m. Living specimens were taken from leaves of *Astelia nadeaudii*, i.e. showing an arboreal way of life (Figure 7).

Remarks This species has been designated as the type species for the genus because it has the most general characters of the four species and might be the closest to a common ancestor.

Nesoropupa fenua n. sp.
Fig. 1C, 2D and 4C

Type material Holotype (MNHN 9936) and one paratype coated for SEM (MNHN 9937).

Type locality Summit of Mt Aorai, alt. 2065 m, Tahiti, 17.61317°S, 149.4952°W.

Material examined A total of 3 specimens. Summit of Mt Aorai, 2065 m, 3 sh (holotype and paratype MNHN) of which one destroyed by SEM manipulation.

Diagnosis A large dextral species of *Nesoropupa*, cylindrically shaped, elevated, without apertural lamellae except a columellar one.

Description (Holotype) Shell small, dextral, cylindrical, thin and fragile, almost translucent. Color brown corneous. 6+ whorls (protoconch broken). Protoconch broken. Surface of postapical whorls rather brilliant, with delicate, radial, oblique, crowded, regularly spaced riblets, ca. 28 per mm on the last whorl. Whorls slightly and regularly convex. Aperture piriform, slightly prosocline, with weakly reflexed margins and thin parietal callus. Apertural teeth reduced to one columellar lamella typical of the genus, but less developed and deeper within the aperture

than for the type species. Umbilicus tiny.

Measurements Dimensions and proportions of 3 adult specimens (two of them with broken protoconch): see Table 2 and Figure 9.

Derivation of name From the Tahitian word "fenua", meaning island, country, property, Earth (Anonymous, 2007; Lemaître, 1995), and by extension nature, heritage. This term is currently used locally for environmental and conservation purposes. Used as a noun in apposition.

Proposed common names Fenua whorl snail (English), Maillot du fenua (French).

Habitat and distribution *Nesoropupa fenua* is only known from its type locality, i.e. the very summit of Mt Aorai, alt. 2065 m, in a patch of *Astelia nadeaudii* in *Metrosideros* scrub mountainous vegetation. It has never been collected alive, the three known dead shells having been sampled from the leaf-litter. This species is most probably arboreal but may also be ground-dwelling.

Remarks The global shape is more cylindrical and the radial ribs finer than in any other species of the genus. Protoconch is unknown as all specimens were broken or seriously damaged at the top. *N. fenua* is the rarest species of the genus, both in terms of number of individuals (biological rarity) and number of localities (ecological rarity).

Nesoropupa nathaliae n. sp.
Fig. 1B, 2C, 4B and 8

Type material Holotype (MNHN 9938), three paratypes of which one coated for SEM (MNHN 9939) and two paratypes (BPBM 282928).

Type locality Summit of Mt Aorai, alt. 2065 m, Tahiti, 17.61317°S, 149.4952°W.

Material examined A total of 52 specimens. Mt Marau, 1430 m, 1 jv; Mt Aorai, 1725 m, 2 sh, 3 jv/fg; Summit of Mt Aorai, 2065 m, 23 sh (holotype and all paratypes), 23 jv/fg.

Diagnosis A medium sized sinistral species of *Nesoropupa*, almost cylindrically shaped, with

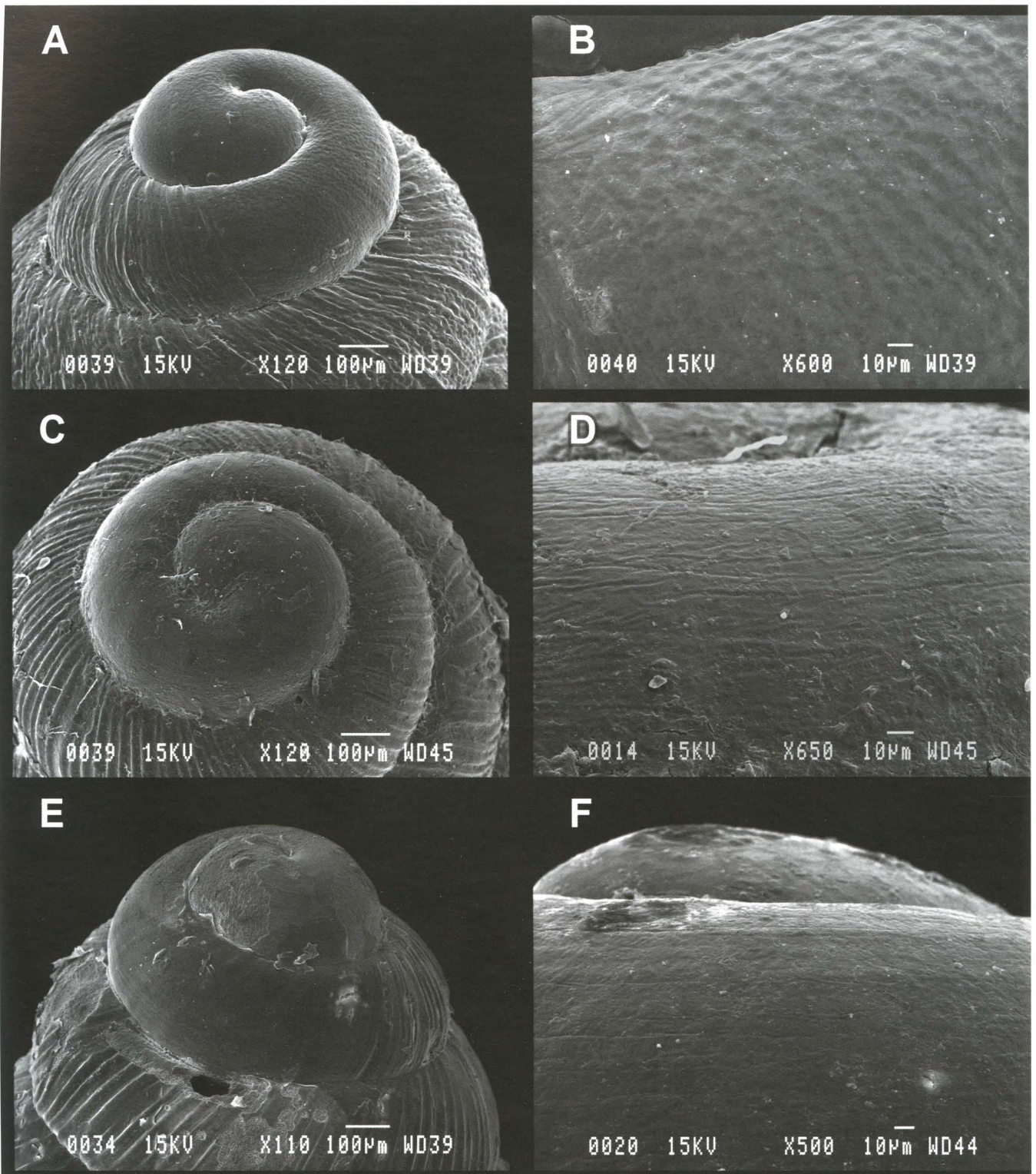


Figure 3 Protoconch and microsculpture of protoconch. **A-B** *Nesopupa* sp. , 6km inside Papeno'o valley, Topatari waterfall (Th29) **C-D** *Nesoropupa duodecim*, Summit of Mt Aorai (Th16) **E-F** *Nesoropupa fontainei*, Summit of Mt Aorai (Th16).

three lamellae: one parietal, one columellar and one lower palatal.

Description Shell very small, sinistral, oval to subcylindrical, thin and fragile, almost trans-

lucent. Color light brown corneous. 7.2 whorls. Protoconch of about 1.85 whorls finely striated with microscopic discontinuous spiral grooves. Transition protoconch/teleoconch rather visible. Surface of postapical whorls typical of the genus,

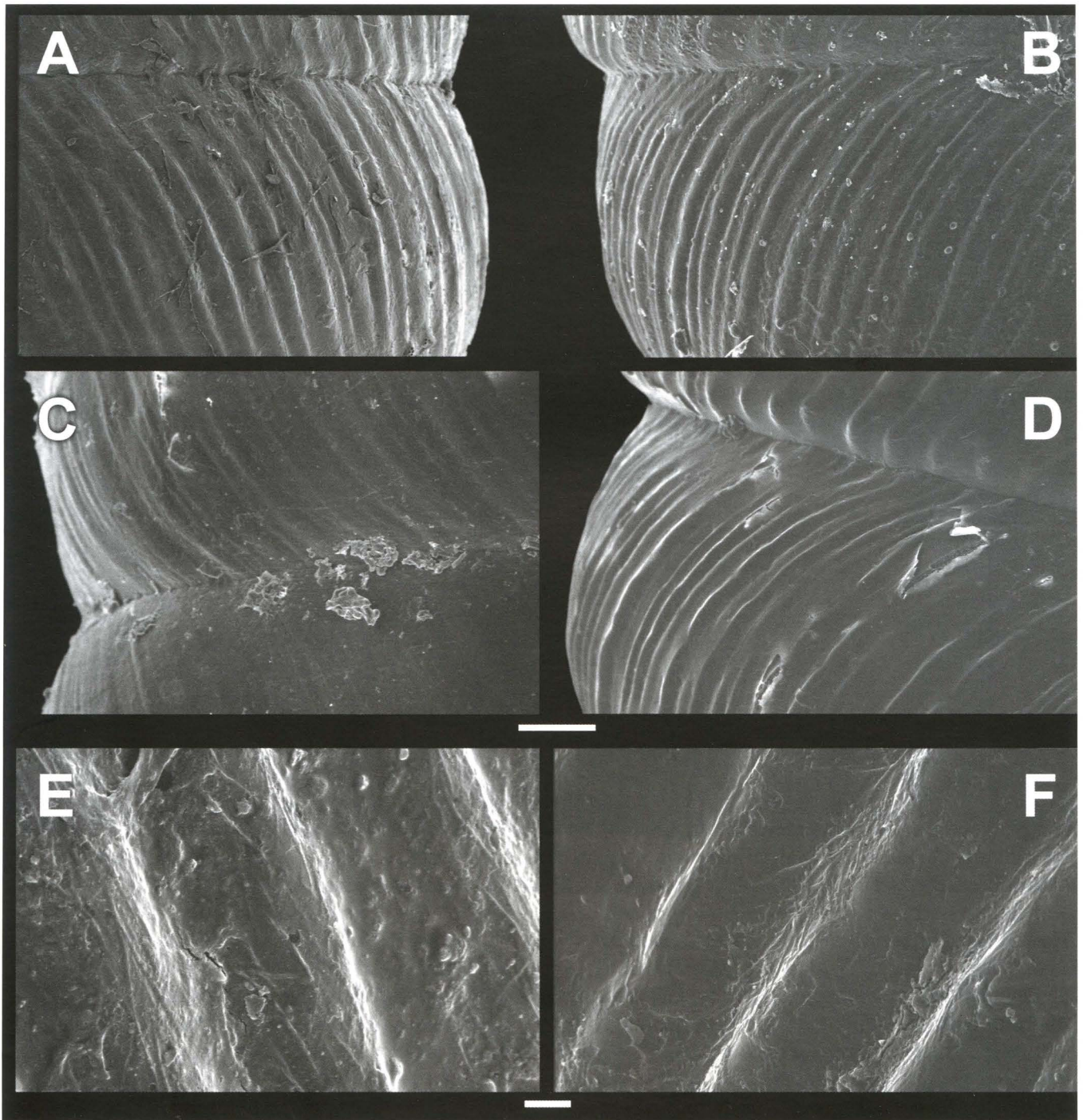


Figure 4 Sculature details of teleoconch. All from summit of Mt Aorai (Th16) except F. **A** *Nesoropupa duodecim* **B** *N. nathaliae* **C** *N. fenua* **D** *N. fontainei* **E** *N. duodecim* **F** *N. fontainei*, Mt Marau (Th05). Scale bars = A-D 100 μ m, E-F 10 μ m.

with ca. 27 ribs per mm on the last whorl. Whorls slightly convex to almost flat with an angular hump overhanging the suture and delimiting a basal crest. Last whorl larger than the previous ones. Aperture sub-rhomboidal to piriform, slightly prosocline, with weakly reflexed margins and thin parietal callus. Three rather thick

and short lamella: one straight parietal lamella in the middle of the parietal wall, being less deeply situated inside the aperture than other lamellae; columellar lamella typical of the genus; one infra-palatal plica. Umbilicus tiny.

Measurements Dimensions and proportions of

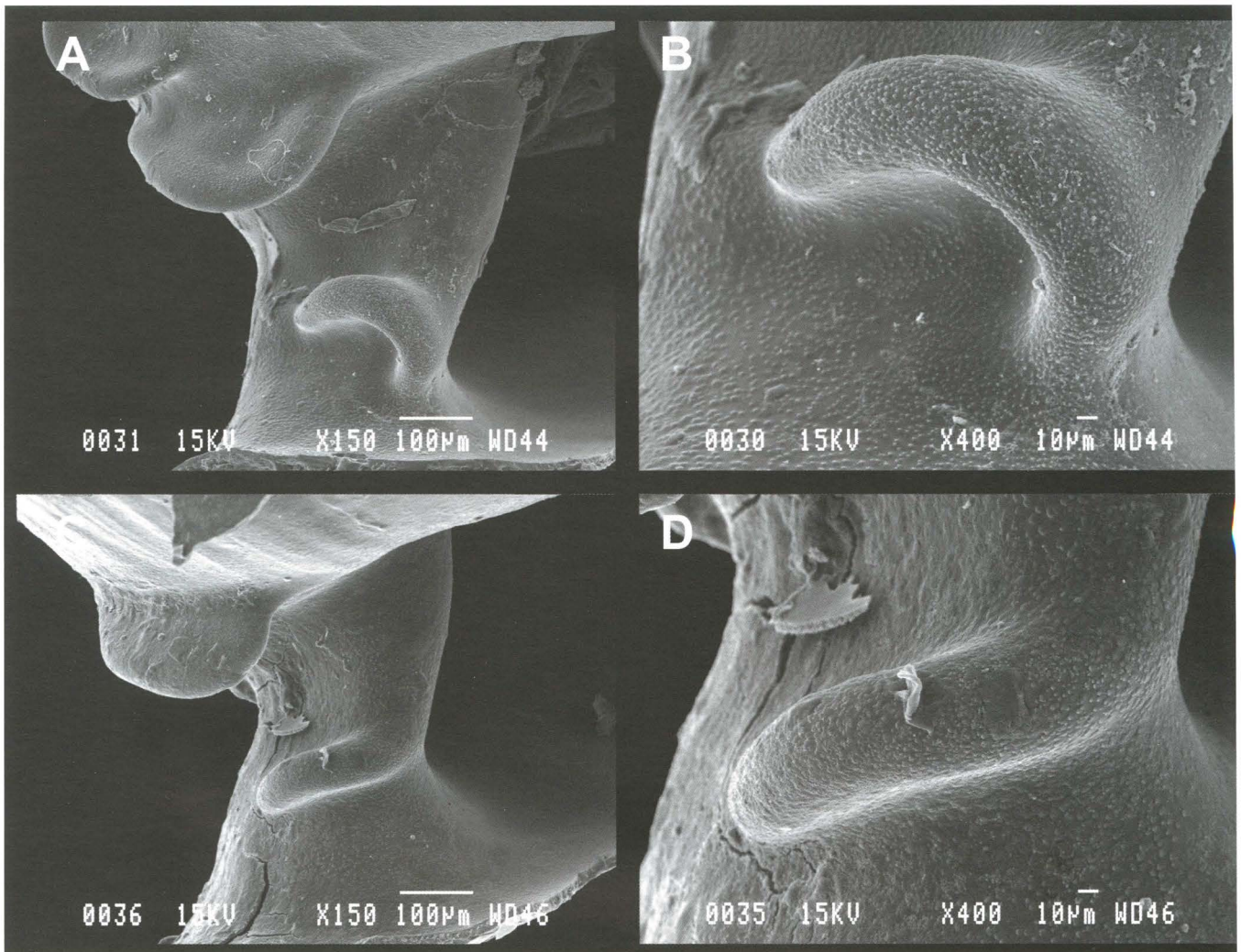


Figure 5 Columellar lamellae and microsculpture of columellar lamellae. **A-B** *Nesopupa* sp., 6km inside Papeno'o valley, Topatari waterfall (Th29) **C-D** *Nesoropupa duodecim*, Summit of Mt Aorai (Th16).

20 adult specimens: see Table 2 and Figure 9.

Derivation of name Named after Nathalie Machon, for her unlimited support and her way to turn life into happiness.

Proposed common names Aorai whorl snail (English), Maillot de l'Aorai (French).

Habitat and distribution *N. nathaliae* is known from Mt Aorai and from a single shell on Mt Marau. It lives in the *Metrosideros* scrub mountainous vegetation, not below 1430 m. Living specimens were taken from *Astelia nadeaudii* leaves, i.e. showing an arboreal way of life (Figure 8).

Remarks Some specimens may have a small supra-palatal lamella reduced to a tubercle (7

out of a total of 23 specimens on the summit of Mt Aorai, i.e. 30%).

The single specimen from Mt Marau, juvenile, may belong to that species, although it is a little larger and less cylindrical.

Nesoropupa fontainei n. sp.
Fig. 1D, 2F, 3E-F, 4D and 4F

Type material Holotype (MNHN 9940), two paratypes (MNHN 9941), one coated paratype (MNHN 9942) and two paratypes (BPBM 282929).

Type locality Tahiti, Mt Aorai, gully just downstream the upper refuge (Fare Ata), where the path cross a stream, alt. 1725 m, 17.59908°S, 149.49652°W.

Material examined A total of 38 specimens. Mt Marau, 1430 m, 1 sh destroyed by SEM manipulation; Mt Aorai, 1520 m, 2 jv/fg; Mt Aorai, 1725 m, 6 sh (holotype, 2 paratypes MNHN, paratypes BPBM), 10 jv/fg; Summit of Mt Aorai, 2065 m, 7 sh (one coated paratype MNHN), 12 jv/fg.

Diagnosis A large sinistral species of *Nesoropupa*, sub-ovate shaped, with two lamellae: one parietal and one columellar.

Description (Holotype) Shell small, sinistral, oval to subcylindrical, thin and fragile, almost translucent. Color brown corneous. 7.6 whorls. Protoconch of about 1.8 whorls finely striated with microscopic discontinuous spiral grooves. Transition protoconch/teleoconch rather visible due to the difference in microsculpture. Surface of postapical whorls typical for the genus, with ca. 22 ribs per mm on the last whorl. Whorls slightly convex with most convexity below the middle to almost flat with an angular hump overhanging the suture and delimiting a basal crest. Last whorl slightly larger than the previous ones. Aperture sub-rhomboidal, angulated on the infrapalatal wall, prosocline, with weakly reflexed margins and thin parietal callus. Two rather thick and short lamellae: one straight parietal lamella in the middle of the parietal wall; columellar lamella typical of the genus; no palatal plica. Umbilicus tiny.

Measurements Dimensions and proportions of 14 adult specimens from Mt Aorai only: see Table 2 and Figure 9.

Derivation of name Named after Dr Benoît Fontaine, friend and colleague in this *Nesoropupa* discovery. These two days spent on Mt Aorai were among the most delightful in our fieldwork experience.

Proposed common names Potbellied whorl snail (English), Maillot ventru (French).

Habitat and distribution *N. fontainei* is known from Mt Aorai and from a single shell on Mt Marau. This mountainous species, living in *Metrosideros* scrub mountainous vegetation, may have an arboreal way of life.

Remarks The single specimen from Mt Marau (fig. 2F, broken after SEM photography) differs from

those of Mt Aorai by its smaller size and slender shell and the little more spaced ribs. It might represent a different subspecies but more material has to be collected. Marau specimen dimensions are: shell height: 3.08mm, shell width: 1.48mm, shell height/width ratio: 2.08, aperture height: 0.9mm, aperture width: 0.84mm.

DISCUSSION

Relationships and zoogeography

The Nesopupinae fauna of the eastern Pacific region encompass four genera (Pilsbry & Cooke, 1918-1920), some of these are illustrated in Figure 6:

1. *Lyropupa* Pilsbry, 1900 (with three subgenera), endemic to the Hawaiian Islands;
2. *Nesopupilla* Pilsbry & Cooke, 1920, endemic to the Hawaiian Islands;
3. *Nesopupa* Pilsbry, 1900 s.l. has a vast distribution from South America (Van Regteren Altena, 1975) to South Africa and easternmost Polynesia (Preece, 1995) with six recognized subgenera, four of them being endemic to a single island (*Cocopupa* Pilsbry & Cooke, 1920, Cocos Island) or archipelago (*Nesodagys* Cooke & Pilsbry, 1920, *Limbatipupa* Cooke & Pilsbry, 1920 and *Infranesopupa* Cooke & Pilsbry, 1920 all from the Hawaiian Islands) in the Pacific;
4. *Pronesopupa* Iredale, 1913, the only genus with toothless aperture, is known from Hawaii, Marquesas, Kermadec and Pitcairn Islands, with two endemic subgenera in Hawaii (*Edentulopupa* Cooke & Pilsbry, 1920 and *Sericipupa* Cooke & Pilsbry, 1920).

Nesoropupa share a number of characters with other Nesopupinae genera or subgenera, but whether this reflects homoplasy or plesiomorphy is purely speculative without molecular data. However, based on the conchological characters used by Pilsbry and Cooke to describe Nesopupinae genera and subgenera (Table 1), it is possible to outline some relationships between them. *Sericipupa*, *Pronesopupa* s.s. and *Edentulopupa* are probably the genera most closely related to *Nesoropupa*. This grouping is supported by the loss of pitted sculpture and the almost complete loss of the angular lamella. Because the loss of pitted sculpture also occurred in an *Afripupa* / *Helanopupa* group, the reduction

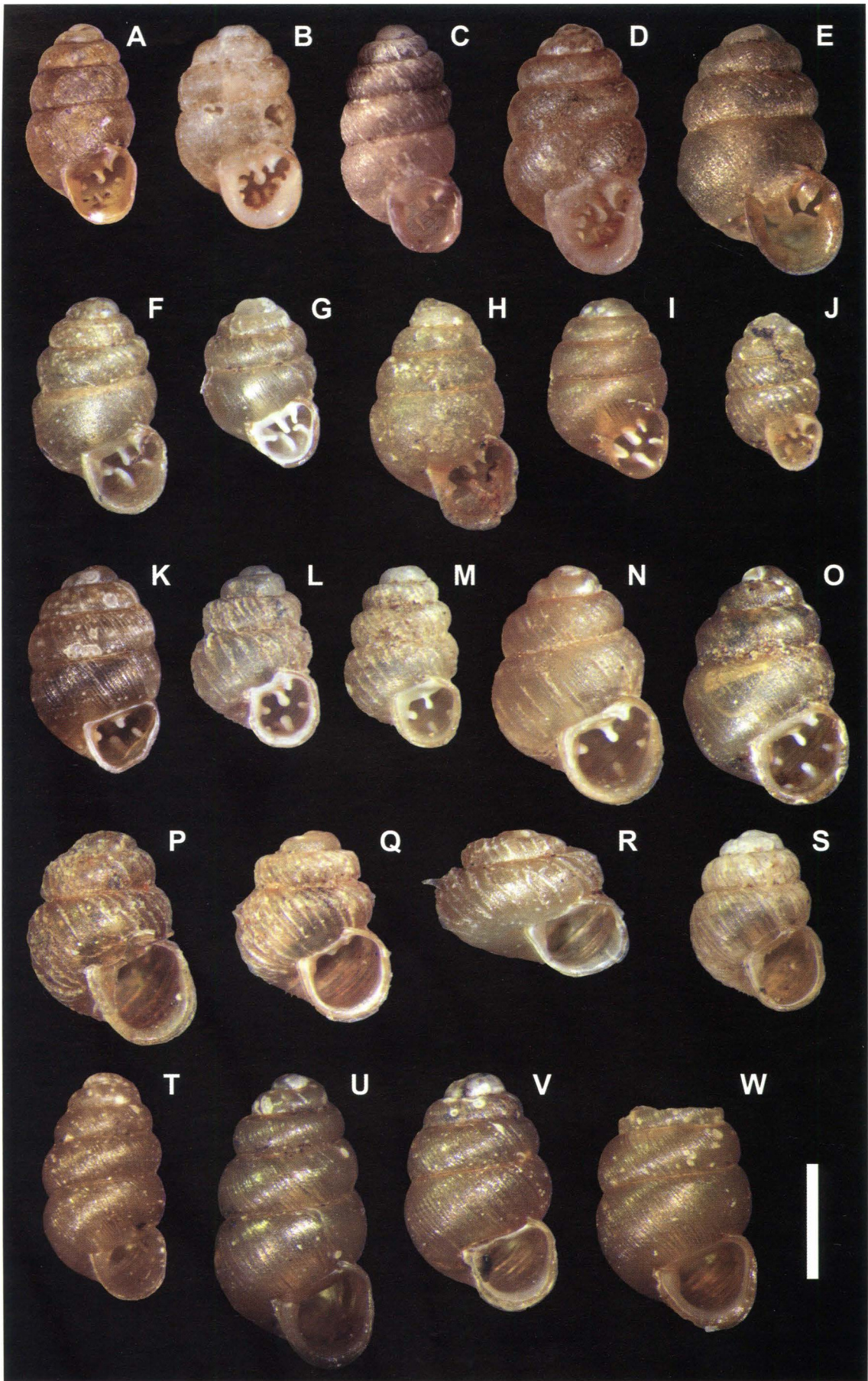




Figure 7 *Nesoropupa duodecim* n. sp. on leaves of *Astelia nadeaudii*, summit of Mt Aorai (Th16).

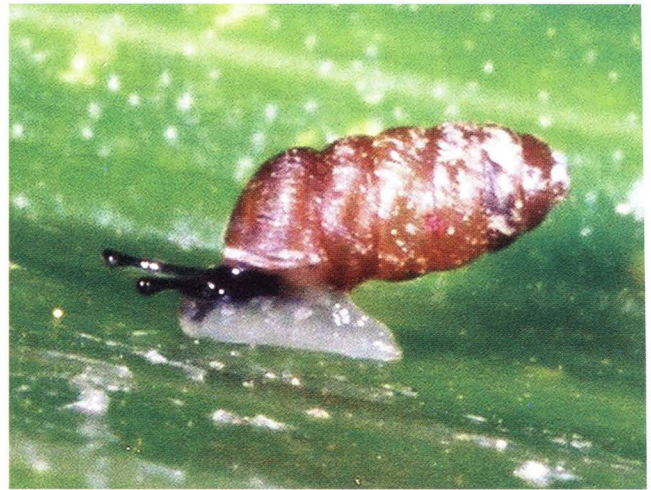


Figure 8 *Nesoropupa nathaliae* n. sp. on leaves of *Astelia nadeaudii*, summit of Mt Aorai (Th16).

of the angular lamella (from an initial state of being curved, then reduced to a straight lamella and completely lost at the end) thus remains the main character that reflects the hypothesized relationships between genera and groups of genera of Nesopupinae. *Limbatipupa*, which is not pitted, has some species with short angular lamella and some without, and thus is the next closest related genus regarding this character.

The importance of the microscopic (discontinuous) spiral sculpture on the protoconch character could not currently be investigated. While all *Nesoropupa* but *N. fenua* have been observed under electronic microscope, it is not known if the spiral sculpture observed in species of other

genera is similar under such magnification. Cooke and Pilsbry (*in* Pilsbry, 1920-1921) separated *Edentulopupa* from *Pronesopupa* s.s. using this character ("minutely striated"); *Nesopupa* (*Limbatipupa*) *alloia* Cooke & Pilsbry, 1920 has "the first [whorl] minutely granulate and very faintly spirally striate". Figure 3 clearly shows that the protoconch micro-sculpture differs radically between *Nesopupa* and *Nesoropupa*.

The inner end of the columellar lamella bent downward is a character shared only by *Nesopupa* s.s. and *Nesopupilla*, while the periost-racial edges on the radial ribs have been reduced or developed in various groups.

Sinistral coiling is common in Vertiginidae;

Figure 6 Nesopupinae of Pacific islands. A *Nesopupa* (*Nesopupa*) *dentifera* MCZ 258352, Aitutaki, Cook Islands, lectotype, sh= 1.75mm; B *Nesopupa* (*Nesopupa*) *paivae* MNHN, Iles Gambier, syntype, sh= 1.8mm; C *Nesopupa* (*Nesopupa*) *pleurophora* NMBE 18861, Marquesas Islands, syntype (from Neubert & Gosteli, 2003: 44, Pl.3 fig.6), sh= 2.0mm; D *Nesopupa* (*Nesopupa*) *armata* MCZ 48315, Borabora Island, Society Islands, holotype, sh= 2.2mm; E *Nesopupa* (*Nesopupa*) *tongana* SMF 1803, Tongatapu, Tonga, lectotype, sh= 2.2mm; F *Nesopupa* (*Nesodagys*) *wesleyana* ANSP 44737, Hilo woods, Hawaii, paratype, sh= 1.9mm; G *Nesopupa* (*Nesodagys*) *thainumi* ANSP 44698, Glenwood, Hawaii, topotype, sh= 1.5mm; H *Nesopupa* (*Cocopupa*) *cocosensis* ANSP 84700 Cocos Island, Pacific Oceans, sh= 2.05mm; I *Nesopupa* (*Infranesopupa*) *limatula* ANSP 44692 Halacakala Crater, Ainahou, East Maui, Hawaii, paratype, sh= 1.6mm; J *Nesopupilla* *waianaensis* ANSP 47560 Pukaloa, Oahu, paratype, sh= 1.4mm; K *Nesoropupa* *duodecim* MNHN 9934 Summit of Mt Aorai, Tahiti, French Polynesia, holotype (see fig. 1A), sh= 1.82mm; L *Nesopupa* (*Limbatipupa*) *newcombi* ANSP 44746, Lanai, Hawaii, sh= 1.6mm, and ANSP 44715, Palolo, Oahu, Hawaii, sh= 1.8mm; M *Nesopupa* (*Limbatipupa*) *singularis* ANSP 44697 Kaliuwavaa, Oahu, paratype, sh= 1.6mm; N *Nesopupa* (*Limbatipupa*) *oahuensis* ANSP 44695 Nuuanu, Luakaha Falls, Oahu, paratype, sh= 2.1mm; O *Nesopupa* (*Limbatipupa*) *kauaiensis* ANSP 44744 Kipu, Kauai, sh= 2.1mm; P *Pronesopupa* (*Pronesopupa*) *senex* ANSP 167560 Sunday Island, Kermadec Islands, sh= 1.9 mm; Q *Pronesopupa* (*Pronesopupa*) *boettgeri* ANSP 46341 Tantalus, Oahu, paratype, sh= 1.7mm; R *Pronesopupa* (*Pronesopupa*) *hystricella* ANSP 46346 Hilo, Hawaii, paratype, sh= 1.3mm; S *Pronesopupa* (*Edentulopupa*) *admodesta* ANSP 46351 Tantalus, Oahu, sh= 1.6mm; T *Pronesopupa* (*Sericipupa*) *frondicola* ANSP 46345 Ainahou, Haleakala, East Maui, paratype, sh= 2.0mm; U *Pronesopupa* (*Sericipupa*) *frondicola corticicola* ANSP 46343 Puanianiau, East Maui, paratype, sh= 2.6mm; V *Pronesopupa* (*Sericipupa*) *lymaniana* ANSP 46342 Olaa, Hawaii, paratype, sh= 2.1mm; W *Pronesopupa* (*Sericipupa*) *sericata* ANSP 46347 Piuhonua, Hawaii, paratype, sh= 2.0mm. Scale bar = 1mm, x 20.

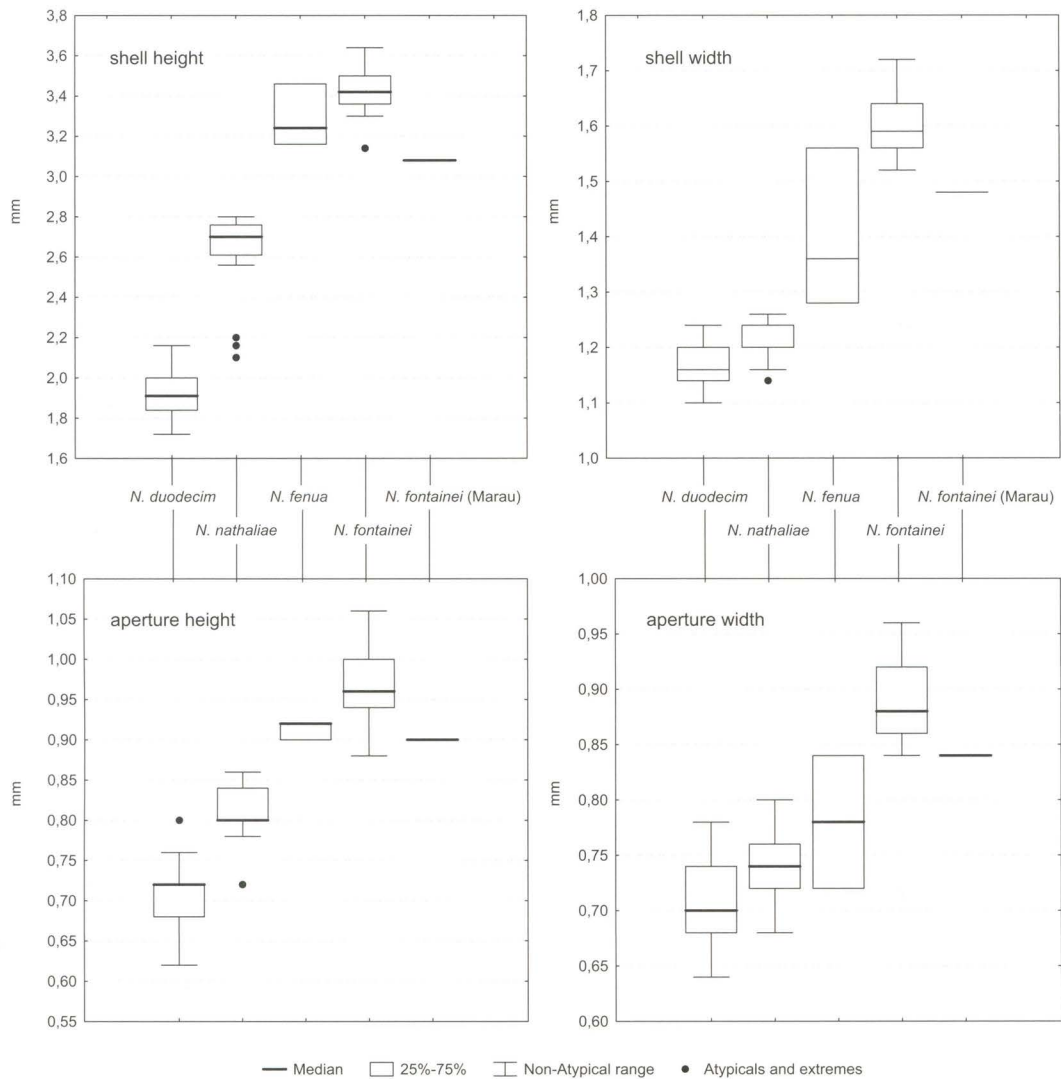


Figure 9 Graphical representation of *Nesoropupa* species measurements.

among Pacific Islands Nesopupinae, it is known to occur in *Lyropupa* in Hawaii, *Cylindrovertilla* in New Caledonia, *Nesopuparia* in Norfolk, and *Nesoropupa* (*Infranesopupa*) *infrequens* Cooke & Pilsbry, 1920 on Kauai, Hawaii Islands.

Genus *Nesoropupa* also has very similar ecological traits as the Hawaiian endemic *Sericipupa* in occurring only in highlands and being arboreal, while the common Pacific vertiginid *Nesoropupa* is mainly soil or rock-dwelling and rarely lives on trees. *Pronesopupa* and *Edentulopupa* live only on barks.

Thus, the distribution and zoogeography of Nesopupinae in the Pacific reflects a complex history of dispersal and speciation in the islands, probably with repeated exchanges between the Hawaiian Islands and south-eastern Polynesia. One possible scenario could be a directional evo-

lution from pitted shells, curved angular lamella, radial striae with periostracal edges, ground-dwelling species, to the very extreme opposite of having lost the pitted sculpture, the lamellae and periostracal edges, becoming more densely ribbed and true arboreal species.

Speciation within *Nesoropupa*

As much of Tahiti is no more than 1.4 million years old (Clouard & Bonneville, 2004), genus *Nesoropupa* most likely represents a very recent radiation on the summits of the island. *Nesoropupa duodecim*, the type species of the genus, is the most common of all four species of the genus, representing 40% of specimens and found at every collecting site containing *Nesoropupa*. Under the hypothesis expressed above (mainly the loss of apertural lamellae as a global trend), it is thought to be conchologically the closest

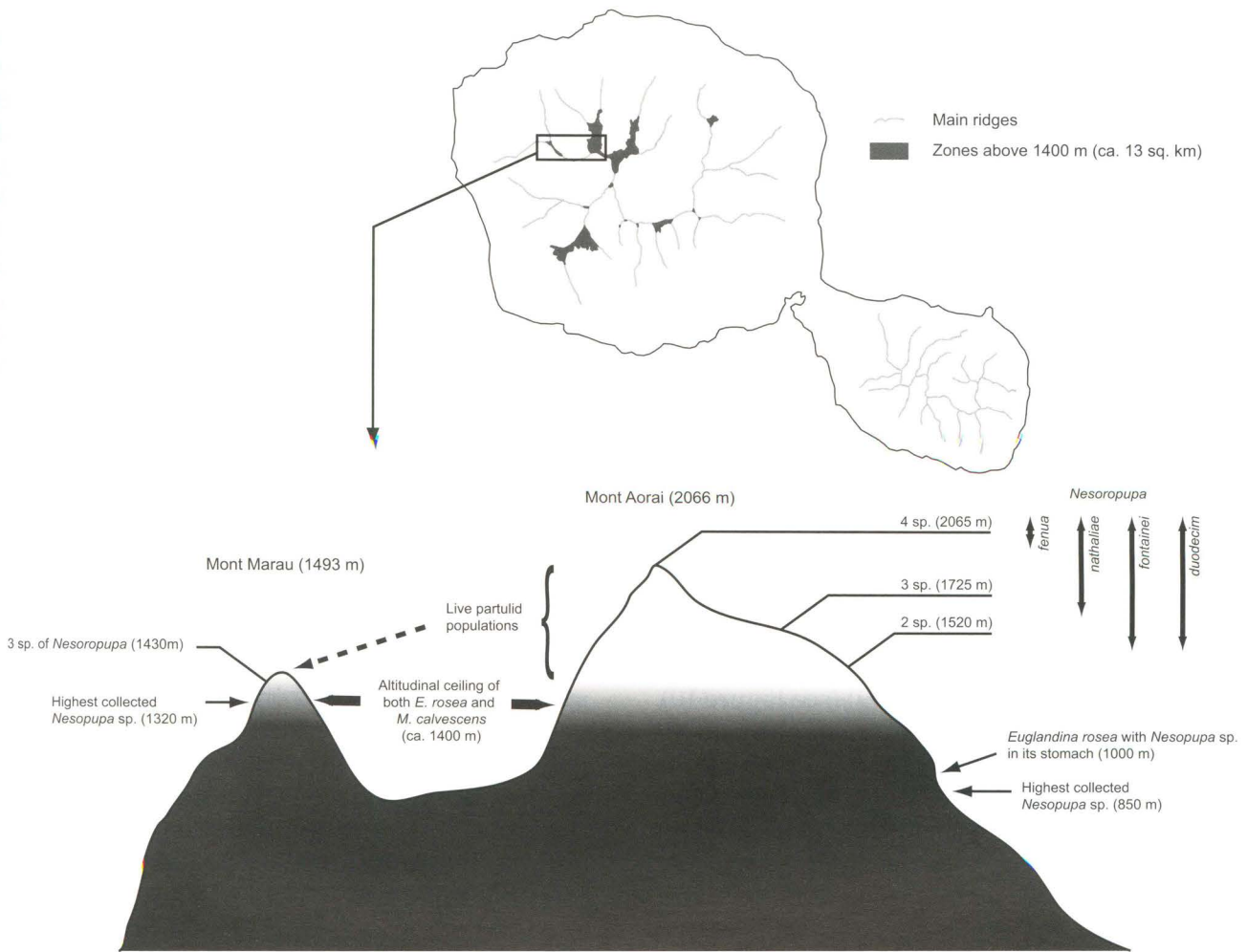


Figure 10 Potential area of occupancy of *Nesoropupa* (zones above 1400 m elevation) on Tahiti and altitudinal chart of native snails and their threats on Mt Aorai and Mt Marau on Tahiti.

from the ancestor. *N. fenua* and *N. fontainei* are thus considered the most derived, and have also much larger shells. The link between these two characters supports the idea of Solem (1976; 1983) according to whom speciation on islands results in an increase in size, and the reduction, to complete loss of apertural lamellae. In that context, both dextral (*N. duodecim*, *N. fenua*) and sinistral (*N. nathaliae*, *N. fontainei*) lineages show increase in size and loss of the lamellae.

Conservation issues

The native flora and fauna on Tahiti in particular, and in Pacific Islands in general, have been severely impacted by exotic species, even in remote places not affected by agriculture or development. However, the high summits of Tahiti are better conserved compared with the lowlands. The mountainous climate prevents the numerous exotic

species that are well established in the lowlands, from climbing to the higher elevations. In particular, dense monotypic patches of *Miconia calvescens*, an invasive tree native from South America that has become one of the major threat to biodiversity by supplanting native forests over the two-thirds of Tahiti, are not recorded higher than 1300 m (Meyer, 1996; Meyer & Florence, 1996), although isolated individuals are observed up to 1400 m on Mt Marau and Mt Aorai (J.-Y. Meyer, pers. com.). Collecting land snails in these monotypic patches has always revealed a very poor fauna, consisting only of introduced species (i.e. Subulinids). Indeed, the large leaves of *Miconia* prevent the formation of suitable litter on the ground.

Also native from America, the snail *Euglandina rosea* was voluntary introduced as a biological control agent against the Giant African snail *Achatina fulica*. It is now well documented that

this predatory snail is not impacting the agricultural pest, but is responsible, or at least the coup de grâce, for the extinction of many endemic partulid land snails in Pacific islands (e.g. Coote & Loeve, 2003). Moreover, experiments in the laboratory (Cook, 1985; 1989), as well as field studies in the Mascarenes (Griffiths, Cook & Wells, 1993) have shown that *Euglandina rosea* preferably feeds on small and ground-dwelling species of gastropods. *Nesoropupa pleurophora* was found in the stomach content of one specimen of *E. rosea* collected on Mt Aorai at 1000 m elevation on Tahiti (Gargominy, 2007). These facts thus suggest that *Euglandina rosea* might have an unrecognized, yet profound impact on minute species.

There is some evidence of an altitude ceiling for *E. rosea*, possibly as a result of low temperatures (Gerlach, 1994). This ceiling, on both Mt Aorai and Mt Marau, is around 1300-1500 m depending on the year (e.g. Coote *et al.*, 1999) (see Figure 10). Such annual variation makes the situation on Mt Marau (1493 m) particularly complex because the summital ridge just reaches this critical elevation. Since the population dynamics of both *E. rosea* and the native land snails are not adequately investigated, it can be speculated that this annual altitudinal ceiling variation explains the persistence of remnant populations of partulids on Mt Marau, because *E. rosea* may not reach the summit each year depending on the lower temperatures. This rhythm, at least until now, might be enough for partulids to be able to maintain a population.

Thus, just as Muratov, Abdou & Bouchet (2005), this paper provides a glimpse of good news on the current fauna of isolated islands: there are still extant populations of endemic species and new species to be described.

However, the strongest optimism should not hide the fact that mountainous species occur on very restricted areas (Figure 10). If we retain as potential areas of occupancy zones higher than 1400 m (suitable vegetation and altitudinal ceiling of exotic species), species of *Nesoropupa* should not occupy more than 13 sq. km spread over a dozen summits or ridges on the main island (Figure 10). Summit *Astelia* shrubland on Mt Aorai is the only habitat where living specimens of *Nesoropupa* were found, and 75% of all specimens were collected here. *N. fenua* was only found in this habitat. It thus seems that it

is the core habitat for the genus, concentrating the main populations of these snails; it does not exceed 2 sq. km in total (Florence, 1993). Species of *Nesoropupa* are all facing an extremely high risk of extinction and meet the criteria to be listed as Critically Endangered CR B1+2abiii on the IUCN Red List (IUCN, 2001).

In this context, some issues are to be addressed. In particular, the effect of global warming should be investigated in order to determine its impact on both the lower altitudinal ceiling of mountainous indigenous species and the upper altitudinal ceiling of introduced species. High elevation areas are so restricted on islands that the rising of isotherms would critically endanger the last remnants of endemic species, both by the decrease of area of occupancy and the arrival of introduced species. Populations of *Nesoropupa* on Mt Marau are very low (less than 8% of the total number of collected specimens, and two species are represented by one shell only), suggesting that the altitudinal refuge is already too degraded and that these populations might well be already extinct (see Figure 10).

Another threat to this fauna is direct human impact. In August 1993, 80% of Mt Orohena from the top edge at 2241 m down to ca. 1950 m on the ridge leading to Pito Hiti was accidentally destroyed by a human-induced fire. Most of the ridge was burned while slopes were less affected. But now the whole site suffers from erosion due to litter destruction and the removal of the structuring trees (J.Y. Meyer and J.F. Butaud, pers. comm.). Such issues suggest a regulation of access to these summits.

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APPENDIX 1

The stations that yielded material of *Nesoropupa*, Tahiti, Society Islands, French Polynesia.

Mt Marau, ridge north of the top transmitter, alt. 1430 m, 17.60691°S, 149.53340°W, *Metrosideros* scrub vegetation, 13 Nov. 2002, O. Gargominy & B. Fontaine (Th05). *N. duodecim*, *N. nathaliae*, *N. fontainei*.

Mt Aorai, path along the ridge between the two refuges (Fare Mato and Fare Ata), alt. 1520 m, 17.59424°S, 149.50002°W, *Metrosideros* scrub vegetation, 15 Nov. 2002, O. Gargominy & B. Fontaine (Th15). *N. duodecim*, *N. fontainei*.

Mt Aorai, gully just downstream the upper refuge (Fare Ata), where the path cross a stream, alt. 1725 m, 17.59908°S, 149.49652°W, *Metrosideros* scrub vegetation, 16 Nov. 2002, O. Gargominy & B. Fontaine (Th17). *N. duodecim*, *N. nathaliae*, *N. fontainei*.

Summit of Mt Aorai, alt. 2065 m, 17.61317°S, 149.49520°W, summit shrubland with *Astelia nadeaudii*, 16 Nov. 2002, O. Gargominy & B. Fontaine (Th16). *N. duodecim*, *N. fenua*, *N. nathaliae*, *N. fontainei*.

APPENDIX 2

Examined Pacific Nesopupinae; generic arrangements follow Pilsbry & Cooke (1918-1920), Pilsbry (1920-1921) and Schileyko (1998).

***Helenopupa* Pilsbry, 1920**

Pupa turtoni E. Smith, 1892 (type species by original designation) - MNHN 9825, St Helena, 5 syntypes (3 sh and 2 fg).

***Nesopupilla* Pilsbry & Cooke, 1920**

Nesopupilla waianaensis Pilsbry & Cooke, 1920 (type species by original designation) - ANSP 47560 Pukaloa, Oahu, 1 paratype (illustrated).

***Cylindrovertilla* O. Boettger, 1880**

Pupa fabreana Crosse, 1872 (type species by original designation) - New Caledonia, Nouméa, Anse Vata. Lectotype (designated by E. Fischer-Piette, 1950, J. de Conch. 50: 81, ICZN 74.5) and 2 paralectotypes MNHN.

Pupa paitensis Crosse, 1872 - New Caledonia, Païta. Lectotype (designated by E. Fischer-Piette,

1950, J. de Conch. 50: 81, ICZN 74.5) MNHN.

***Nesoropupa* Pilsbry, 1900**

Type species *Pupa (Vertigo) tantilla* Gould, 1847 by original designation

Vertigo armata Pease, 1871 - Bolabola [Borabora Island, Society Islands], lectotype (designated by Cooke & Pilsbry in Pilsbry & Cooke 1918-1920: 328) MCZ 48315 (illustrated) and 43 paralectotypes MCZ 31398.

Vertigo dentifera Pease, 1871 - Roratonga [error for Aitutaki, Cook Islands, teste Garrett (1881: 401), who collected the specimens], lectotype (designated by R.I. Johnson, 1994, Bull. Mus. Comp. Zool. 154(1): 11) MCZ 258352 (illustrated) and 5 paralectotypes MCZ 48314.

Pupa paivae Crosse, 1865 - Iles Gambier, 6 syntypes (1 illustrated), MNHN 9943.

Pupa tongana O. Boettger, 1880 - Tonga: Tongatapu, "lectotype" (from SMF label) SMF 1803 (material not examined, photograph send by E. Neubert).

Pupa pleurophora Shuttleworth, 1852 - Marquesas Islands, syntype NMBE 18861 (material not examined, photograph send by E. Neubert, see Neubert & Gosteli, 2003: 44, Pl.3 fig.6).

***Nesoropupa (Cocopupa)* Pilsbry & Cooke, 1920**

Vertigo cocosensis Dall, 1900 (type species by monotypy) - ANSP 84700 Cocos Island, Pacific Oceans, 2 sh (1 illustrated) and 2 fg.

***Nesoropupa (Nesodagys)* Cooke & Pilsbry, 1920**

Nesoropupa wesleyana Ancey, 1904 (type species by subsequent designation) - ANSP 44737, Hilo woods, Hawaii, 6 paratypes (4 sh and 2 fg).

N. thaanumi Ancey, 1904 - ANSP 44698, Glenwood, Hawaii, 7 sh "topotypes" (1 illustrated); ANSP 44684, Glenwood, Hawaii, 10+ sp.

***Nesoropupa (Limbatipupa)* Cooke & Pilsbry, 1920**

Pupa newcombi L. Pfeiffer, 1852 (type species by original designation) - ANSP 44746, Lanai, Hawaii, coll. C.M. Cooke, 2 sh (1 illustrated); ANSP 44715, Palolo, Oahu, Hawaii, coll. C.M. Cooke, 5 sh (1 illustrated).

Nesoropupa oahuensis Cooke & Pilsbry, 1920 - ANSP 44695 Nuuanu, Luakaha Falls, Oahu, 5 paratypes (1 illustrated).

N. singularis Cooke & Pilsbry, 1920 - ANSP 44697 Kaliuwavaa, Oahu, 5 paratypes (1 illustrated).

N. kauaiensis Ancey, 1904 - ANSP 44744 Kipu, Kauai, 7 sh (1 illustrated).

Nesopupa (Infranesopupa) Cooke & Pilsbry, 1920

Nesopupa limatula Cooke & Pilsbry, 1920 (type species by original designation) - ANSP 44692 Halacakala Crater, Ainaho, East Maui, Hawaii, 1 paratype (illustrated).

Pronesopupa Iredale, 1913

Pronesopupa senex Iredale, 1913 (type species by monotypy) - ANSP 167560 Sunday Island, Kermadec Islands, 1 sh (illustrated).

P. boettgeri Cooke & Pilsbry, 1920 - ANSP 46341 Tantalus, Oahu, 3 paratypes (1 illustrated).

P. boettgeri spinigera Cooke & Pilsbry, 1920 - ANSP 46348, Luakaha, Nuuanu, Oahu, 5 paratypes.

Pronesopupa hystricella Cooke & Pilsbry, 1920 - ANSP 46346 Hilo, Hawaii, 5 paratypes (1 illustrated).

Pupa acanthinula (Ancey, 1892) - ANSP 378250 and ANSP 378251, Hawaii.

Pronesopupa (Edentulopupa) Cooke & Pilsbry, 1920

Pupa admodesta Mighels, 1845 (type species by original designation) - ANSP 44779 Outside rim Tantalus bowl, southwest Oahu, 5 sh and 4 fg; ANSP 44781 Western ridge of Popouwela, Oahu, Hawaii, 2 sp; ANSP 44780 Pauoa slope of Tantalus, Castle Trail, Oahu, Hawaii, 1 sp; ANSP 46351 Tantalus, Oahu, 3 sh (1 photographed); ANSP 46352 Luakaha, Nuuanu, Oahu, 1 sp.

Pronesopupa (Sericipupa) Cooke & Pilsbry, 1920

Pronesopupa (Sericipupa) frondicola Cooke & Pilsbry, 1920 (type species by original designation) - ANSP 46345 Ainahou, Haleakala, East Maui, 1 paratype (illustrated).

Pronesopupa (Sericipupa) frondicola corticicola Cooke & Pilsbry, 1920 - ANSP 46343 Puanianiau, East Maui, 1 paratype (illustrated).

Pronesopupa (Sericipupa) lymaniana Cooke & Pilsbry, 1920 - ANSP 46342 Oloo, Hawaii, 1 paratype (illustrated).

Pronesopupa (Sericipupa) sericata Cooke & Pilsbry, 1920 - ANSP 46347 Piihonua, Hawaii, 2 paratype (fg) (1 illustrated).

Pronesopupa (Sericipupa) orycta Cooke & Pilsbry, 1920 - ANSP 46344 Palihonkapapa, Hawaii, 1 paratype (fg).