Snails found among herbarium specimens of Galapagos lichens and bryophytes, with the description of *Scolodonta rinae* (Gastropoda: Scolodontidae), a new species of carnivorous micro-mollusk

SERGIO E. MIQUEL¹ & FRANK BUNGARTZ²

 Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, (1405) Ciudad Autónoma de Buenos Aires, República Argentina. Consejo Nacional de Investigaciones Científicas y Técnicas.
 Adjunct Scientist, Charles Darwin Foundation for the Galapagos Islands; Curator of Lichens, School of Life Sciences, PO Box 874501, Arizona State University, Tempe, AZ 85287-4501, U.S.A. (frank.bungartz@gmail.com)
 Corresponding author: F. Bungartz.

Abstract. For the first time we document several species of micro-mollusks in the Galapagos inhabiting lichens and bryophytes, possibly using them as part of their diet. Eight species of micro-mollusks were found as a by-catch among 10% of 400 herbarium specimens collected throughout the archipelago. Nine species of lichens and 6 of bryophytes were inhabited. The endemic *Pupisoma galapagorum* was the most common micro-mollusk, particularly frequent among *Heterodermia*, occasionally found on *Cyphellostereum*, *Squamidium nigricans*, and among hepatics (*Frullania, Bryopteris*). Other micro-mollusks were *Tornatellides chathamensis*, *Pupisoma dioscoricola, Helicina* sp., and *Succinea* sp. Examination of the digestive tract of *P. galapagorum* detected green algae, hyphae, spores, and fragments of bryophyte leaves (possibly *S. nigricans*). This endemic micro-mollusk apparently uses lichens and bryophytes not only for shelter but also as food. Another snail found repeatedly is a predator, described here as *Scolodonta rinae* n. sp. It is a member of Scolodontidae, a Neotropical family considered endemic to continental South America, and here for the first time documented from the Galapagos. *Pupisoma galapagorum*, previously known from Floreana, Isabela, San Cristóbal, and Santa Cruz, is reported also from Pinta and Santiago. *Ambrosiella floreanae*, previously considered endemic to Floreana, is reported from Santa Cruz.

Key words. Ecological interactions, land snail, microhabitats, food-chain.

DOI. https://doi.org/10.1127/arch.moll/146/173-186

Introduction

The Galapagos Islands support a heterogeneous group of terrestrial gastropods; nearly 120 species have so far been reported, although the majority, c. 100 species, belong to the Bulimulidae (PARENT et al. 2014). Species of this family are generally medium-sized (about 10 mm); others, commonly called micro-mollusks, measure only 1–5 mm (PARENT & COPPOIS 2009, PARENT et al. 2014, MIQUEL & HERRERA 2014).

The preferred habitat of terrestrial Galapagos snails is the ground, where they can be found beneath decomposing trunks, branches, and among fallen leaves. Generally, snails inhabit more humid habitats of the Galapagos; in drier areas they are occasionally also found under rocks or in hollows where the humidity is higher than in the immediate vicinity. Very few species have been collected on other substrates: *Tornatellides chathamensis* (Dall, 1892) has been reported from fern fronds (DALL & OCHSNER 1928, PARENT & COPPOIS 2009, MIQUEL & HERRERA 2014), and *Pupisoma galapagorum* Pilsbry, 1934 inhabits nests of Darwin's finches (Thraupidae: Geospizini; MIQUEL et al. 2015).

Field observations suggest that terrestrial gastropods are frequently associated with lichens and bryophytes, using them for shelter and occasionally as food (e.g., Lichens: PEAKE & JAMES 1967, COKER 1967; Bryophytes: PILSBRY 1948, WILLIAMSON & CAMERON 1976, WIESEN-BORN 2003). Some of the earliest observations interpret damage on crustose lichen thalli in Jamaica as grazing patterns caused by snails (PLITT 1934). In temperate (e.g., Ireland: ANDERSON 1997; Baltic region: BAUR & BAUR 1997) and Mediterranean climates (Negev Desert: SHACHAK et al. 1987, YOM-TOV & GALUN 1971) snails have not only been observed to feed on lichens and bryophytes, but several studies experimentally confirmed snail herbivory on lichens (LAWREY 1983, FRÖBERG et al. 1993, 2001, ROSSO & MCCUNE 2003, GAUSLAA et al. 2006, VATNE et al. 2010) and mosses (SZLAVECZ 1986, OYESIKU & OGUNKOLADE 2006).

ceived attention; the first checklist of this overlooked group was only recently published (MIQUEL & HERRERA 2014). Habitat requirements of these minute snails are still poorly known, but field observations suggest that some species may regularly be associated with lichens

In the Galapagos, micro-mollusks have rarely re-

Table 1. Micro-mollusk species found among herbarium specimens of lichen and bryophyte collected in the Galapagos (sorted according to the number of snail specimens associated with herbarium material; *denotes a specimen packet that contains both a lichen and bryophyte).

	Island									
	Santa Cruz	Isabela	Floreana	Santiago	San Cristóbal	Pinta	Pinzón			
Lichens										
H. verrucifera	<i>P. galapagorum,</i> <i>S. rinae</i> n. sp.	P. galapagorum	P. galapagorum	P. galapagorum						
H. leucomela ssp. leucomela		P. galapagorum	P. galapagorum	P. galapagorum						
<i>H. leucomela</i> ssp. <i>boryi</i>		P. galapagorum								
H. galactophylla	P. galapagorum									
H. podocarpa					P. galapagorum					
Sticta dichotoma s.l.	A. floreanae	<i>Helicina</i> sp., <i>T. chathamensis</i>								
*Cyphellostereum sp. 1 ined.	P. galapagorum									
Lobaria patinifera	<i>Succinea</i> sp.									
Parmotrema internexum				P. galapagorum						
Leptogium punctulatum					P. galapagorum					
Bryophytes	L									
Bryophyta (mosses)										
Squamidium nigricans	P. dioscoricola	P. galapagorum		P. galapagorum		P. galapagorum				
Brachymenium systylium	<i>Succinea</i> sp.						Gastrocopta sp.			
Weissiodicranum insularum	Succinea sp.									
Hepatophyta (liverworts)	•									
Bryopteris filicina	P. galapagorum			P. galapagorum						
*Frullania aculeata	P. galapagorum									
Other Substrates	•									
Fern fronds (Dall & Ochsner 1928, Miquel & Herrera 2014)					T. chathamensis					
Finch nests (MIQUEL & HERRERA 2014)	P. galapagorum				P. galapagorum					
On the ground (MIQUEL & HERRERA 2014)	<i>Helicina</i> sp., <i>P. galapagorum,</i> <i>S. rinae</i> n. sp.									

Table 2. Number of micro-mollusk specimens found not closely associated with lichens or bryophytes during the September 2013 field survey at Los Gemelos (Santa Cruz, Galapagos) (*4 specimens destroyed by squash preparation to examine radula and digestive tract; †species so far not found among lichens or bryophytes; coordinates of the collection sites: no. 25: 0°37'44.9'S, 90°23'16.5" W, 613 m; no. 26: 0°37'44.2" S, 90°23'16.5" W, 612 m; no. 27: 0°37'43.6" S, 90°23'15.4" W, 616 m; no. 28: 0°37'43.3" S, 90°23'14.5" W, 610 m).

	Species									
Collection site no.	Pupisoma galapagorum	[†] <i>Habroconus</i> sp. aff. <i>H. (P.) pacificus</i>	[†] Cecilioides consobrina	† Opeas pumilum	<i>Scolodonta rinae</i> n. sp	Total of specimens				
25	ICCDRS 40579: 1	ICCDRS 40578: 4	ICCDRS 40580: 3	ICCDRS 40581: 2	ICCDRS 40582: 15	25				
26	—	_	ICCDRS 40576: 9	ICCDRS 40575: 2	ICCDRS 40577: 5	16				
27	—	_	—	—	ICCDRS 40583: 8*	8				
28	ICCDRS 0040571: 5	_	ICCDRS 40572: 1	ICCDRS 40573: 2	ICCDRS 40574: 3	11				
Total of specimens	6	4	13	6	31	60				

and/or bryophytes and possibly even feed on them. If particular species of micro-mollusks are indeed regularly associated with lichens or bryophytes, one might expect that these species will inadvertently be trapped as a by-catch together with specimens collected for the herbarium. Therefore we decided to survey herbarium specimens of lichens and bryophytes collected as part of the Galapagos Biodiversity Inventory (BUNGARTZ et al. 2013, GRADSTEIN & ZIEMMECK 2014, ZIEMMECK & HARPEL 2014) for the presence of micro-mollusks.

Materials and Methods

Surveying herbarium material

In a preliminary assessment, c. 30 dried herbarium specimens were screened at random and examined for snails. [Most herbarium specimens are hosted at the herbarium of the Charles Darwin Foundation (CDS), one also at the University of Colorado Museum of Natural History (COLO); acronyms listed follow *GRBio* (http://grbio. org/).] No micro-mollusks could be found among crustose lichens or thallose liverworts. We assume that, if micromollusks live on these species, they do not adhere well to their surface and are easily lost during collection procedures. Subsequently therefore, our search focused only on foliose and fruticose lichens, leafy liverworts, and mosses.

A total of 400 of these structurally more complex herbarium specimens were examined, of which 231 (58%) were lichens and 169 (42%) bryophytes (for an overview see Table 1; for all material examined the snail specimens isolated from herbarium material are cited; more detailed collection data can be found online at http://www.darwinfoundation.org/datazone/collections/). This herbarium material was collected and identified as part of the biodiversity inventory of Galapagos lichens and bryophytes (BUNGARTZ et al. 2013, GRADSTEIN & ZIEMMECK 2014, ZIEMMECK & HARPEL 2014).

Each lichen and bryophyte specimen was carefully examined for micro-mollusks collected as a by-catch using a stereoscopic microscope (Zeiss Stemi DV4). Micro-mollusks were removed, identified and subsequently accessioned into the Invertebrate Collection of the Charles Darwin Foundation (ICCDRS), Puerto Ayora, Galapagos, Ecuador.

Squash preparations of snails

To study the contents of the digestive tract of the 2 most frequently found snail species, 3 specimens of each were rehydrated in tap water for 2 h and then squashed in a water droplet placed on a microscope slide, applying gentle pressure to the cover-slip, thus crushing the shell to reveal the rehydrated soft tissues. Although no fresh snail specimens were examined, rehydrating the material worked unexpectedly well. Before being deposited in the herbarium, lichens and bryophytes are routinely dried at 40-45 °C in a conventional plant dryer for at least 2 d. During that process snails trapped as a by-catch were apparently preserved inadvertently in a more or less "mummified" stage.

At the research station in the Galapagos the squash preparations were examined with a compound microscope [Zeiss Axio-Imager.A1 equipped with differential interference contrast (DIC)]. Because squashing completely destroyed the material, we examined only 3 specimens of *Pupisoma galapagorum*: 2 from the most commonly inhabited lichen species [ICCDRS 40476 from *Hetero-dermia verrucifera* (Kurok.) W.A. Weber (CDS 31624), and ICCDRS 40483 from *H. leucomela* ssp. *leucomela* (CDS 31796)], and 1 from the most frequently inhabited bryophyte, *Squamidium nigricans* (Hook.) Broth. (ICCDRS 40493 = CDS 28040).

For comparison, we similarly also examined 3 specimens of the carnivorous micro-mollusk *Scolodonta rinae* (ICCDRS 40583).

Collecting fresh snail specimens

To test if some of the snails found during the herbarium survey would generally be more frequently associated with lichens or bryophytes than with other substrates, a few selected sites on Santa Cruz where herbarium specimens had been collected were subsequently revisited in September 2013; these 3 sites were: (1) Miconiashrubland along the footpath from Bella Vista to El Puntudo, (2) upper transition-zone forest of Mina Granillo Rojo, and (3) disturbed Scalesia pedunculata forest around Los Gemelos. At these sites lichens and bryophytes were closely inspected for snails; other habitats typically inhabited by micro-mollusks (leaf litter, tree logs, fallen branches, soil depressions, etc.) were also carefully screened. All snail specimens collected during these surveys were subsequently identified and accessioned into the ICCDRS (Table 2).

Taxonomic studies

The snail specimens isolated from the herbarium material and the fresh reference material were studied in detail at the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina). There, selected specimens were measured using a ball-micrometer, splutter-coated with gold-palladium (using a Quorum Technologies SC7620 splutter coater), and photographed with a scanning electron microscope (PHILIPS XL series 30, high vacuum). The dried specimens were returned and accessioned into the ICCDRS.

Results

Surveying herbarium material

Table 1 summarizes the results of surveying herbarium specimens for micro-mollusks. A total of 8 snail species

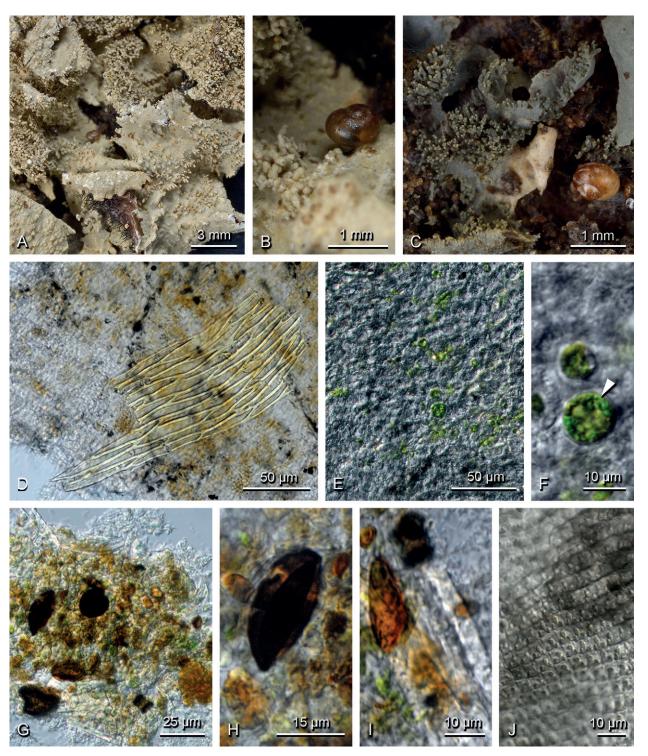


Figure 1. Light micrographs of *Pupisoma galapagorum* isolated from herbarium specimens. **A**, **B**. On thallus lobes between isidia of *Parmotrema internexum* (Aptroot, A. 65545; CDS 32134 = ICCDRS 40541): (**A**) general view; (**B**) detail. **C**. On thallus lobes between isidia of *Leptogium punctulatum* (Bungartz, F. 6675; CDS 34911= ICCDRS 40537). **D**. Squash preparation with animal cells and a fragment of a moss leaf (specimen isolated from *Squamidium nigricans* [Ziemmeck, F. 797; CDS 28040 = ICCDRS 40493]). **E–I.** Squash preparations (specimen isolated from *H. leucomela* ssp. *leucomela* [Aptroot, A. 65210; CDS 31796 = ICCDRS 40483]): (**E**) animal cells from the intestinal tract mixed with green algae; (**F**) close-up (arrow: chloroplast with a wavy outline characteristic of the lichen photobiont *Trebouxia*); (**G**) animal cells from intestinal tract mixed with filamentous cells (possibly hyphae), chlorococcoid green algae (globose green cells, possibly *Trebouxia*), trentepohlioid green algae (orange clusters of irregular cells, possibly *Trentepohlia*), deep brown fungal spores (degenerated, some as fragments); (**H**) close-up of a fungal spore (possibly from *Heterodermia*, a genus with brown ascospores; the spore in part degenerated, details no longer distinct); (**I**) close-up of unpigmented strands (hyphae?) and brown spore fragments. **J.** Close-up of the radula, minute squares with droplet-shaped notches, indicative of a herbivorous snail (specimen isolated from *S. nigricans*, Ziemmeck, F. 797 [CDS 28040 = ICCDRS 40493]).

were discovered among the 400 collections of herbarium specimens examined; 5 species of micro-mollusks were found in 23 (10%) of the 231 lichen packets, and 4 species of micro-mollusks were retrieved from 9 (5%) of the 169 bryophyte packets. In the majority of cases, only a single snail was detected, but in 1 instance 7 individual snails were isolated from 1 herbarium specimen.

Snails were most commonly found on 5 species of lichens of the genus *Heterodermia* Trevis., most frequently *H. verrucifera* and *H. leucomela* (Fée) Swinscow & Krog. Next most commonly, snails were found on a species of *Sticta* (Schreb.) Ach. (here referred to as *Sticta dichotoma* s.l., although, with the revision of Galapagos Lobariaceae still under way, this identification must be considered preliminary; *S. dichotoma* Bory s.str. does not occur in the Galapagos and the material likely belongs to an undescribed endemic species), and on *Cyphellostereum* sp. 1 (an undescribed basidiolichen typically growing on liverworts, particularly the genus *Frullania* Raddi.).

Snails were also found on 3 moss species—Weissiodicranum insularum Reese, Brachymenium systylium (Müll.Arg.) A. Jaeger and Squamidium nigricans—and on 2 liverwort species—Bryopteris filicina (Sw.) Nees and Frullania aculeata Taylor (same packet as the lichen specimen of Cyphellostereum sp. 1). Micro-mollusks were found in 9 packets of H. verrucifera, in 5 packets of S. nigricans and in 3 packets of H. leucomela ssp. leucomela (Fée) Swinscow & Krog.

Pupisoma galapagorum was the most common snail species, of which 9 specimens were discovered on *H.* verrucifera. The new records of *P. galapagorum* from Santiago and Pinta extend its known distributions to these islands. The second most common species was a species of *Succinea*. It was found in 10% of the herbarium packets examined that contained snails: in 1 packet of *Weissiodicranum* Reese, 1 of *Brachymenium* Schwäger., and 1 of *Lobaria* (Schreb.) Hoffm. Other species were single finds of *Tornatellides chathamensis* and *Helicina* sp. on *S. dichotoma* s.1. (from Alcedo, Isabela), and *P. dioscoricola* and *Ambrosiella floreanae* on *S. nigricans* and *S. dichotoma* s.1. (from Santa Cruz).

Squash preparations of snails

Two specimens of *P. galapagorum* (isolated from lichens: ICCDRS 40476 & ICCDRS 40483) contained green algae, hyphae and over-mature degenerated spores (Fig. 1E–I). Due to the preparation technique, the exact location of the material inside the snail's digestive tract could not be determined, but algal cells, hyphae and spores were all found in close proximity to the radula of the snail. No such material (algae, hyphae or spores) was found in the squash made from a snail isolated from the moss *S. nigricans* (ICCDRS 40493). Instead we observed a bryophyte leaf fragment, structurally identical to the apical part of leaves of *S. nigricans* [see Fig. 1D; compare with the drawing in SPESSARD-SCHUETH (1994: 723, fig. 538d)].

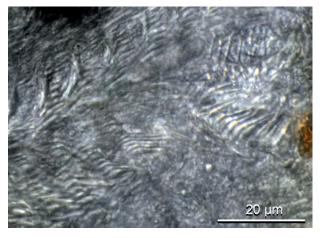


Figure 2. Light micrograph of *Scolodonta rinae* squash, showing fragments of the radula with the spiny teeth typical of a carnivorous snail (ICCDRS 40583) (final image of 2 microphotos taken at different focal planes, combined via focus blending).

Only animal tissue, from the squashed snail itself and possibly its diet, but no algae, bryophyte fragments or fungal material was discovered in squash preparations of *S. rinae*; the radula of this animal is consistent with other species in this family of carnivorous snails (ICCDRS 40583, Fig. 2).

Collecting fresh snail specimens

During the field survey in September 2013 several snail species were found, apparently not closely associated with lichens or bryophytes: *P. galapagorum, Habroconus* sp. aff. *H. (Pseudoguppya) pacificus, Cecilioides consobrina, Opeas pumilum,* and *S. rinae* (Table 2). At Los Gemelos, *S. rinae* was found to be unusually abundant: 31 out of 60 specimens collected. For the other snail species, a comprehensive list with collection details has already been published in MIQUEL & HERRERA (2014). It is not repeated here, but the distribution map includes all new records from Santa Cruz (Fig. 3B).

Of the species found, only *P. galapagorum* and *S. rinae* had previously been discovered also among herbarium specimens. The other species collected in the field are all apparently not closely associated with lichens or bryophytes. Only *P. galapagorum* was found regularly among lichens and bryophytes, although this snail species was occasionally also encountered on the ground, among leaf litter. In the field *S. rinae* could not be found closely associated with lichens or bryophytes, but the vicinity of its collection sites was frequently littered with empty *Pupisoma* shells.

Taxonomic studies

The carnivorous *Scolodonta rinae* is described here new to science, followed by a newly revised, more detailed

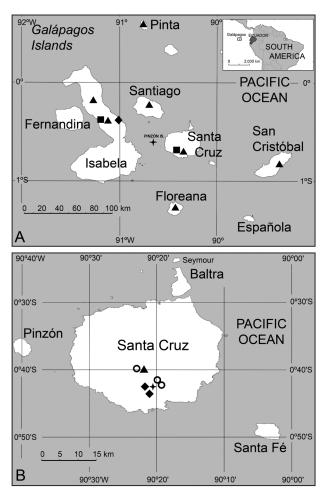


Figure 3. New records of Galapagos micro-mollusks. A. Overview of the archipelago with the following species: ■*Helicina* sp.; ◆*Tornatellides chathamensis*; ▲*Pupisoma galapagorum;* + *Gastrocopta* sp. B. New records on Santa Cruz: O*Ambrosiella floreanae*; ◆ *Succinea* sp.; ▲ *Pupisoma dioscoricola*; + *Scolodonta rinae* n. sp.

description of *Ambrosiella floreanae*. For all other species the list includes only a summary of habitat preferences (if known), distribution, and affinity to lichens and bryophytes:

Scolodontidae Baker, 1925

Scolodonta Doering, 1875

Scolodonta rinae n. sp.

Figures 2, 3B, 4A-G

Holotype. ICCDRS 40519: 1 dried specimen (shell & body) isolated from herbarium material of *Heterodermia verrucifera* by S.E. Miquel & F. Bungartz [Ecuador: Galapagos. Santa Cruz: above Mina Granillo Rojo on the N side of the island, W of the dirt road along the quarry. $0^{\circ}37'4.5''$ S, $90^{\circ}21'59.1''$ W, 628 m alt., transition zone, open and dry forest of mainly *Psidium galapageium*, with some *Scalesia pedunculata* and *Piso-nia floribunda*, and basalt outcrops; specm. isolated from herbarium material of *H. verrucifera* that was collected on bark growing among hepatics (*Frullania* sp.) on a semi-shaded, wind- and rain-sheltered, east-facing trunk of *Zanthoxylum fagara*, 23-Sep-2013, leg. F. Bungartz 10959 (CDS 54922)].

Paratypes [all collected in the field, not isolated from herbarium material, stored as dried specimens (shell & body)]: ICCDRS 40520 [Ecuador: Galapagos. Santa Cruz: Los Gemelos, 0° 37' 41.9" S, 90° 23' 15.9" W, 626 m alt., humid zone, young, moderately open to widely open Scalesia pedunculata forest, invaded by blackberry (Rubus nivea) that has recently been controlled by herbicide treatment, 23-Sep-2013, leg. F. Bungartz & S.E. Miquel]; ICCDRS 40521 [ibid.: 23-Sep-2013, leg. F. Bungartz & S.E. Miquel]; ICCDRS 40522 [Santa Cruz: trail from Media Luna to El Puntudo, approx. halfway along the path, 0°39'0.0" S, 90°19'35.6" W, 513 m alt., humid zone, Miconia robinsoniana shrubland, sparsely invaded by Cinchona pubescens (invasive trees killed by herbicide treatment), on the ground, below tree trunks, 27-Sep-2013, leg. F. Bungartz & S.E. Miquel]; ICCDRS 40523 [ibid.: trail from Media Luna to El Puntudo, about halfway along the path, on the ground, below tree trunks, 27-Sep-2013, leg. F. Bungartz & S.E. Miquel].

Description. Shell very small, very thin, with 4 brilliantly polished, translucent, olivaceous whorls; spire depressed but slightly rounded; embryonic and adult whorls with suture with well-defined sculpture of numerous radiating, slightly flexuous, indented varices and lines of growth; last whorl evenly rounded, base smooth, convex; with a narrow deep umbilicus, clearly showing all of the coils; aperture oblique, descending, hardly expanded, peristome sharp and thin. Internal wall covered by numerous pustules, more numerous on the columellar wall; the pustules are strongly acuminated. Radula with aciculiform teeth, 20-1-20 (of the ∞ –C– ∞ type).

Measurements of Holotype. 1.40×0.75 mm, 4 whorls (Fig. 4B).

Measurements of a Paratype. 1.15×0.55 mm, 3 whorls (ICCDRS 40521) (Fig. 4D).

Comparison. The new species has a shell similar to that of *Scolodonta semperi* Doering, 1875, but is much smaller (e.g., 1.40×0.75 mm, 4 whorls vs. 3.0×1.3 mm, $4\frac{1}{2}-5$ whorls; see HYLTON SCOTT 1945, MIQUEL & AGUIRRE 2011). The radula of *S. rinae* has 20-1-20 teeth while *S. semperi* shows 12-1-C-1-12 teeth (HYLTON SCOTT 1945); only the latero-marginal teeth of *S. rinae* are typically aciculiform (Fig. 2). The number of whorls of the shell of *S. rinae* suggests that the holotype selected here is an adult.

Etymology. Dedicated to Peruvian malacologist Rina Ramírez Mesías, world-renowned specialist on Scolodontidae.

Distribution and habitat. Only known from Santa Cruz, first observed among decaying lichens and liver-

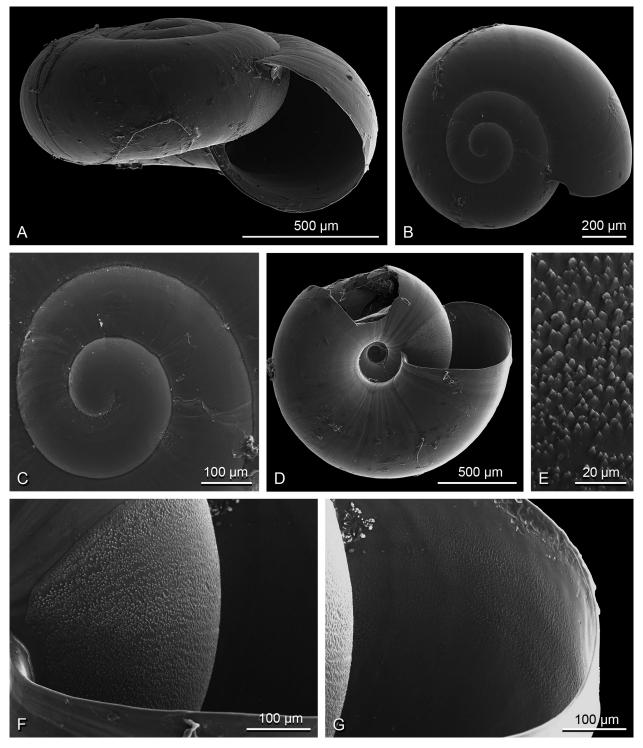


Figure 4. Scanning electron micrographs of *Scolodonta rinae* n. sp. A. Holotype $(1.40 \times 0.75 \text{ mm}, 4 \text{ whorls}; \text{ICCDRS 40519});$ B, C. Paratype (ICCDRS 40521): (B) general morphology; (C) detail of the protoconch $(1.15 \times 0.55 \text{ mm}, 3 \text{ whorls})$. D–G. Ibid. (ICCDRS 40523): (D) umbilical view; (E) umbilical wall densely covered with minute teeth; (F) umbilical and labral wall; (G) labral wall.

worts, subsequently also found on soil and litter, among plant roots.

Affinity to lichens and liverworts. The holotype was isolated from *H. verrucifera*, but this predatory snail is not necessarily closely associated with lichens or bryophytes; it apparently feeds on micro-mollusks that use them as their habitat (see Discussion).

General comments. No representatives of this family have previously been recorded in the Galapagos. The *Scalesia. pedunculata* forests at Los Gemelos, where the paratype specimens were collected, are among the last remnants of this forest type on Santa Cruz. Today these forests are highly disturbed by the presence of introduced species, both plants (e.g., blackberry, *Rubus nivea*

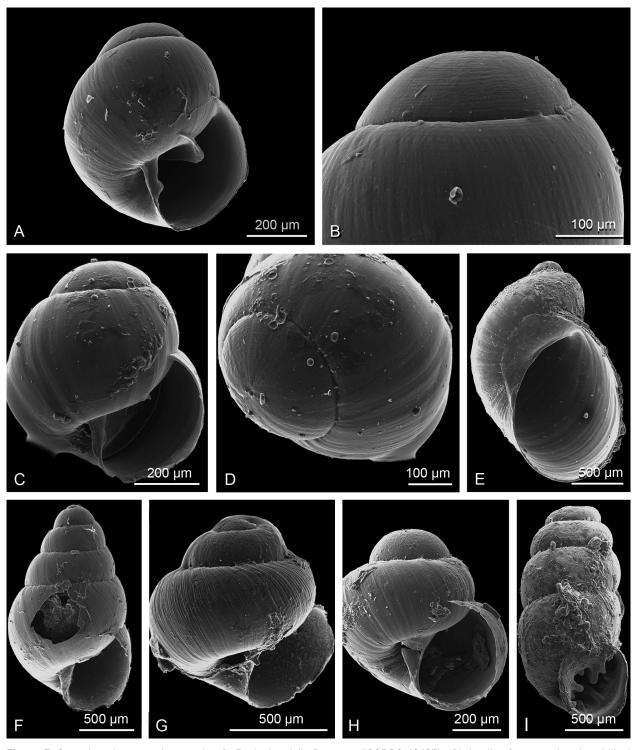


Figure 5. Scanning electron micrographs. **A**, **B**. *Ambrosiella floreanae* (ICCDRS 40497): (**A**) details of apertural and umbilical areas; (**B**) detail of protoconch (2.0 × 1.2 mm, 5 whorls). **C**, **D**. *Helicina* sp. (ICCDRS 40514): (**C**) shell morphology; (**D**) detail of protoconch. **E**. *Succinea* sp. (2.35 × 1.45 mm, 2¼ whorls; ICCDRS 40518). **F**. *Tornatellides chathamensis* (1.95 × 1.20 mm, 5 whorls; ICCDRS 40515). **G**. *Pupisoma dioscoricola* (0.65 × 0.80 mm, 2.25 whorls; ICCDRS 40517). **H**. *Pupisoma galapagorum* (0.95 × 0.95 mm, 2¾ whorls; ICCDRS 40485). **I**. *Gastrocopta* sp. [2.00 × 1.00 mm, > 4 whorls (apex broken); ICCDRS 40516].

Thunb.) and animals (e.g., the African gastropod *Lissa-chatina fulica* (Bowdich, 1822); see MIQUEL & HERRERA 2014). The fauna of other micro-mollusks recorded at this site consists of only a few endemic species. *Scolodonta rinae* makes up just over half of the total specimens of micro-mollusks collected at Los Gemelos (Table 2). For

the current nomenclatural arrangement of the genus *Scolodonta* see BREURE & MIQUEL (2012).

Other specimens examined. ICCDRS 40524: 31 specms (19 dry + 12 in alcohol) [Ecuador: Galapagos. Santa Cruz: El Puntudo, 0° 38' 42.2" S, 90° 19' 55.1" W, 692 m alt., humid zone, 27-Sep-2013, leg. X. Pilataxi & S.E. Miquel];

ICCDRS 40574: 1 juv. specm. & 2 fragms [ibid.: Los Gemelos, 0° 37' 43.3" S, 90° 23' 14.5" W, 610 m alt., humid zone, 3-Oct-2014, leg. S.E. Miquel]; ICCDRS 40577: 5 specms [ibid., 0° 37' 44.2" S, 90° 23' 16.5" W, 612 m alt., humid zone, 3-Oct-2014, leg. S.E. Miquel]; ICCDRS 40582: 15 specms [ibid., 0° 37' 44.9" S, 90° 23' 16.5" W, 613 m alt., humid zone, 3-Oct-2014, leg. S.E. Miquel]; ICCDRS 40583: 4 specms [ibid., 0° 37' 43.6" S, 90° 23' 15.4" W 616 m alt., humid zone, 3-Oct-2014, leg. S.E. Miquel].

Achatinellidae Gulick, 1873

Ambrosiella Odhner, 1963

Ambrosiella floreanae Miquel & Herrera, 2014

Figures 3B, 5A, B

Ambrosiella floreanae MIQUEL & HERRERA 2014: 112, figs 8–10, map 3.

Revised description. Shell with slightly convex whorls, perforate; suture rather deep; aperture somewhat oblique, parietal edge with a medial, sharp and concave lamella; columella straight, with 1 lamella, growth lines faintly marked; color uniformly brown, protoconch with slightly and closely spiral costulae (previously not documented).

Measurements of holotype. 2.50×1.30 mm, 6 whorls (ICCDRS 36992).

Distribution and habitat. The first record for Santa Cruz; originally described as endemic to Floreana, where it was collected in open grasslands ("Pampa de Alviar").

Affinity to lichens and liverworts. *Ambrosiella* generally prefers humid habitats; isolated from *Sticta*, a lichen genus common throughout the Galapagos humid zone.

Specimen examined. Isolated from lichen bryophyte. ICCDRS 40497: 1 specm. from *Sticta dichotoma* s.l. [Ecuador: Galapagos. Santa Cruz: Los Gemelos, E crater (old specm.; coordinates unknown), 500 m alt., humid zone, 17-Jun-1976, leg. Sipman s.n. (L-63484, COLO 297952)].

Helicinidae Férussac, 1822

Helicina Lamarck, 1799

Helicina sp.

Figures 3A, 5C, D

Taxonomic comment. Several species of this genus have been reported from the Galapagos (MIQUEL & HERRERA 2014). Unfortunately the single specimen found during our survey of herbarium specimens could not be assigned here with certainty to any one of these species.

Distribution and habitat. Species of *Helicina* in the Galapagos are known from the humid zone of Floreana,

Isabela, San Cristóbal, Santa Cruz, Pinta, Santiago; generally from a wide range of habitats, for example in agricultural areas of Isabela and San Cristóbal, on Floreana also within the boundaries of the national park (*Sc. pedunculata*-forest of Cerro Pajas), on Santa Cruz at an urban site (Bellavista) (see MIQUEL & HERRERA 2014).

Affinity to lichens. Like most micro-mollusks *Helicina* prefers humid habitats; isolated here from *Sticta*, but specimens from many other substrates suggest this species is not generally associated with lichens.

Specimen examined. Isolated from lichen. ICCDRS 40514: 1 juv. specm. from *Sticta dichotoma* s.l. [Ecuador: Galapagos. Isabela, Alcedo: on crater rim near the hut, 0°26'33" S, 91°5'31"W, 1100 m alt., humid zone, 7-Mar-2006, leg. Aptroot 65223 (CDS 31809)].

Succineidae Beck, 1837

Succinea Draparnaud, 1801

Succinea sp.

Figures 3B, 5E

Taxonomic comment. The 3 specimens of this snail found during the survey of herbarium material could only be identified here to genus. Most species of *Succinea* become larger than a few millimeters and are typically not considered micro-mollusks. The 3 snails found among herbarium specimens were, however, minute (Fig. 5E) and thus insufficiently well developed to be determined to species.

Distribution and habitat. In the Galapagos, species that belong to the genus *Succinea* are common on a variety of substrates, in the upper transition and humid zones of Santa Cruz, San Cristóbal, Floreana, Isabela, Fernandina, Pinzón, Pinta, and Santiago (DALL & OCHNSNER 1928, PARENT et al. 2014).

Affinity to lichens and bryophytes. On herbarium specimens of *Weissiodicranum insularum* (on the ground), and *Brachymenium systylium* and *Lobaria patinifera* (both epiphytic); all 3 are characteristic elements of transition zone forests.

Specimens examined. Isolated from lichen: ICCDRS 40499: 1 specm. from *Lo. patinifera* [Ecuador: Galapagos. Santa Cruz: above Mina Granillo Rojo, 0°37'4.5" S, 90°21'59.1" W, 628 m alt., transition zone, 23-Sept-2013, leg. Bungartz 10949 (CDS 54924)]. Isolated from bryophytes. ICCDRS 40518: 1 specm. from *W. insula-rum* [ibid.: trail from Puerto Ayora to Bellavista (historic specm.; coordinates unknown), 100 m alt., transition zone, 17-Jun-1976, leg. Sipman M-169 (CDS 46085)]; ICCDRS 40498: 1 specm. from *Bra. systylium* [ibid.: halfway between Puerto Ayora and Bellavista, 0°42'40" S, 90°19' 24" W, 135 m alt., transition zone, 25-Feb-2006, leg. Aptroot 64635 (CDS 31209)].

Tornatellides Pilsbry, 1910

Tornatellides chathamensis (Dall, 1892)

Figures 3A, 5F

Leptinaria chathamensis DALL 1892: 98. Tornatellides chathamensis Dall — MIQUEL & HERRERA 2014: 110, figs 5–7, map 3.

Distribution and habitat. Fernandina, Floreana, Isabela, Pinzón, San Cristóbal, Santa Cruz, and Pinta; throughout the humid zone, common in agricultural areas of San Cristóbal and Santa Cruz, in Floreana also in *Scalesia* forest (C. Pajas); on Isabela found in open grassland along the crater rim (Sierra Negra), on Santa Cruz in *Miconia* scrub (MIQUEL & HERRERA 2014); DALL & OCHSNER (1928) previously reported the species from fern fronds.

Affinity to lichens. Isolated from *Sticta* collected on Alcedo, Isabela; specimens from many other substrates suggest the species is not closely associated with lichens; records from fern fronds indicate that it tolerates slightly drier habitats than other micro-mollusks.

Specimen examined. ICCDRS 40515: 1 specm. from *S. dichotoma* s.l. [Ecuador: Galapagos. Isabela, Alcedo: on crater rim near the hut, 0°26′33″S, 91°5′31″W, 1100 m alt., humid zone, 7-Mar-2006, leg. Aptroot 65223 (CDS 31809)].

Vallonidae Morse, 1864

Pupisoma Stoliczka, 1873

Pupisoma (Ptychopatula) Pilsbry, 1889

Pupisoma (Ptychopatula) dioscoricola (C.B. Adams, 1845)

Figures 3B, 5G

Helix dioscoricola C.B. ADAMS 1845: 16.
Pupisoma (P) dioscoricola (C.B. Adams) — MIQUEL & HERRERA 2014: 115, figs 20–22, map 5.

Distribution. Jamaica (type locality), United States (Florida and Texas), from the Caribbean to southern Brazil and northern Argentina, some records probably anthropogenic (HAUSDORF 2007); Galapagos: Fernandina, San Cristóbal, Santa Cruz, Floreana (agricultural areas), Isabela (endemic Guava forest on Alcedo) and Santa Cruz (disturbed sites in the National Park) (MIQUEL & HERRERA 2014).

Affinity to bryophytes. Isolated from *Squamidium nigricans*; collected in one of the oldest *Scalesia pedunculata* forests of Santa Cruz (among the last sites still characterized by ancient *Scalesia* trees).

Specimen examined. Isolated from bryophyte. ICCDRS 40517: 1 specm. from *S. nigricans* [Ecuador: Galapagos. Santa Cruz: old and abandoned farm of Don Benito, ca. 1 km NE of El Puntudo. 0°38'25.0" S, 90°19'55.0" W,

718 m alt., humid zone, 8-Feb-2007, leg. Ziemmeck 1082 (CDS 33077)]

Pupisoma (Pupisoma?) galapagorum Pilsbry, 1934

Figures 1A-J, 3A, 5H

Pupisoma galapagorum PILSBRY 1934: 114, pl. 16, figs 7–9.
Pupisoma (Pupisoma?) galapagorum Pilsbry — MIQUEL & HERRE-RA 2014: 115, figs 18–19, map 3.

Taxonomic comment. Although HAUSDORF (2007) treated *P. galapagorum* as a synonym of *P. comicolense* Baker, 1928, based on a comparative study of their shells, we consider the Galapagos specimens sufficiently different to be considered an endemic of this archipelago. Particularly the new record from Pinta (Fig. 3A) suggests that the Galapagos material is not identical with specimens found in continental South America.

Distribution and habitat. Floreana, San Cristóbal, Isabela and Santa Cruz, throughout the upper transition zone, both in agricultural areas outside the National Park (e.g., on Isabela), at heavily disturbed sites (e.g., on Santa Cruz: *Scalesia pedunculata* forests at Los Gemelos, strongly invaded by blackberry; mixed *Pisonia–Scalesia* forests of Mina Granillo Rojo, threatened by gravel mining), and at sites that are today well protected (e.g., *Scalesia pedunculata* forests of Floreana); the specimens from Santiago and Pinta constitute the first records from these islands.

Affinity to lichens and liverworts. *Pupisoma galapa-gorum* was the snail species most frequently found among lichen and bryophyte specimens. It is particularly common on *Heterodermia* and *Squamidium nigricans* (Table 1) but has also been found on other substrates. Unlike most other micro-mollusks, the species apparently tolerates relatively dry habitats and has for example been reported from finch nests (see MIQUEL & HERRERA 2014). The species uses lichens as part of its diet (see Discussion).

Specimens examined. Isolated from lichens. Heterodermia verrucifera. ICCDRS 40474: 1 specm. [Ecuador: Galapagos. Santa Cruz: dirt road to Mina Granillo Rojo, 0°36'56.6"S, 90°22'2.7"W, 583 m alt., transition zone, 21-Oct-2007, leg. Ertz 11563 (CDS 36889)]. ICCDRS 40482: 1 specm. [ibid.: 0°37'5.8"S, 90°21' 59.1"W, 617 m alt., transition zone, 21-Oct-2007, leg. Ertz 11584 (CDS 36910)]. ICCDRS 40475: 2 specms [ibid.: midway between Puerto Ayora and Canal de Itabaca, 0° 37' 24.0" S, 90° 24' 49.0" W, 575 m alt., humid zone, 17-Feb-2005, leg. Tehler 8675 (CDS 40638)]. ICCDRS 40477: 4 specms [ibid.: near Los Gemelos, 0°36'31.0" S, 90°22'4.0" W, 350 m alt., humid zone, 28-May-2005, leg. Aptroot. 63223 (CDS 29958)]. ICCDRS 40476: 3 specms (one destroyed by squash) [Isabela, Alcedo: outer SE-exposed slope, 0° 27' 29.0" S, 91°7'19.0" W, 1089 m alt., humid zone, 5-Mar-2006, leg. Aptroot 65042 (CDS 31624)]. ICCDRS 40480: 1 specm.

[Isabela, Darwin: above Tagus Cove, 0°13'28.2" S, 91° 19'17.9" W, 872 m alt., transition zone, 15-Nov-2007, leg. Bungartz 7753 (CDS 38259)]. ICCDRS 40478: 2 specms [Floreana: W-slope of C. Alieri, 1°17'24.1"S, 90°27'8.9"W, 347 m alt., transition zone, 12-Jan-2011, leg. Bungartz 9315 (CDS 46541)]. ICCDRS 40479: 1 specm. [ibid.: between C. de los Chanchos and C. de los Burros, 1°16'40.3" S, 90°24'12.4" W, 311 m alt., transition zone, 21-Jan-2011, leg. Bungartz 10007 (CDS 47376)]. ICCDRS 40481: 1 specm. [Santiago: along trail from Bucanero to Jaboncillos, 0°12'9.0" S, 90°47'3.0" W, 796 m alt., transition zone, 23-Mar-2006, leg. Bungartz 4734 A (CDS 28845)]. From H. leucomela ssp. leucomela. ICCDRS 40483: 3 specms (1 specm. destroyed by squash) [Isabela, Alcedo: on crater rim, near the hut. 0° 26' 33.0" S, 91°5'31.0"W, 1000 m alt., humid zone, 07-Mar-2006, leg. Aptroot 65210 (CDS 31796)]. ICCDRS 40484: 1 juv. specm. [Floreana: on W-slope of C. Alieri, 1°17'24.1"S, 90°27'8.9"W, 347 m alt., transition zone, leg. Bungartz 9316 (CDS 46542)]. ICCDRS 40486: 1 juv. specm. [ibid. Asilo de la Paz, C. Wittmer, 1°18'50.0" S, 90°27'13.8" W, humid zone, 03-Jan-2010, leg. Hillmann GAL-120 (CDS 44879)]. ICCDRS 40485: 1 juv. specm. [Santiago: along trail from Bucanero to Jaboncillos, 0°12'9.0"S, 90°47'3.0"W, 796 m alt., transition zone, 23-Mar-2006, leg. Bungartz 4740 (CDS 28851)]. From H. leucomela ssp. boryi. ICCDRS 40487: 1 specm. [Isabela, Alcedo: outer SE-exposed slope, 0°27'29.0"S, 91°7'19.0"W, 1000 m alt., humid zone, 5-Mar-2006, leg. Bungartz 4042 (CDS 27972)]. From Heterodermia podocarpa. ICCDRS 40488: 1 specm. [San Cristóbal: trail to C. Pelado, 0° 51' 51.0" S, 89° 27' 36.4" W, 402 m alt., transition zone, 23-Aug-2008, leg. Truong 1520 (CDS 39831)]. From H. galactophylla. ICCDRS 40489: 1 specm. [Santa Cruz: abandoned farm of Don Benito, 0°38'25.0"S, 90° 19′ 55.0″ W, 718 m alt., humid zone, 8-Feb-2007, leg. Bungartz 5609 (CDS 33067)]. From Cyphellostereum sp. 1. ICCDRS 40496: 1 specm. [Santa Cruz: trail from Bellavista to Media Luna, 0°39'57"S, 90°19'31.2"W, 531 m alt., humid zone, 23-Sep-2013, leg. Bungartz (CDS 54929); the packet also contains F. aculeata]. From Parmotrema internexum (Nyl.) Hale ex DePriest & B.W. Hale. ICCDRS 40541: 1 juv. specm. [Santiago: permanent plot no. 8, 0°12'18" S, 90°47'4" W, 814 m alt., humid zone, 24-Mar-2006, leg. Aptroot 65545 (CDS 32134)]. From Leptogium punctulatum Nyl. ICCDRS 40537: 1 juv. specm. [San Cristóbal: between C. Pelado and C. Partido, 0°41'50" S, 89°27'38" W, 383 m alt, transition zone, 28-Apr-2007, leg. Bungartz 6675 (CDS 34911)]. Isolated from bryophytes. Squamidium nigricans. ICCDRS 40493: 2 specms (1 specm. destroyed by squash) [Isabela, Alcedo: outer SE-exposed slope, 0° 27' 29.0" S, 91° 7' 19.0" W, 1089 m alt., humid zone, 5-Mar-2006, leg. Ziemmeck 797 (CDS 28040)]. ICCDRS 40492: 1 specm. [Pinta: near volcano in south-central part (historic specm.; coordinates unknown), 600 m alt., humid zone, 11-Jul-1976, leg. Gradstein M-365 & Sipman (CDS 10701)]. ICCDRS 40494:

2 specms [Santiago: trail from La Central to La Bomba, 0°14'10.0" S, 90°44'42.0" W, 690 m alt., transition zone, 25-Mar-2006, leg. Ziemmeck 1035 (CDS 29058)]. ICCDRS 40495: 1 specm. [Isabela, Alcedo: outer SEexposed slope, 0°26'16.0" S, 91°4'36.0" W, 798 m alt., transition zone, 7-Mar-2006, leg. Ziemmeck 898 (CDS 28294)]. From *Bryopteris filicina*. ICCDRS 40490: 1 specm. [Santa Cruz: from Bellavista to Garrapatero, 0°41'12.0" S, 90°18'22.0" W, 214 m alt., humid zone, leg. Ziemmeck 701 (CDS 27599)]. ICCDRS 40491: 1 specm. [Santiago: trail from Bucanero to Jaboncillos, 0°12'9.0" S, 90°47'3.0" W, 796 m alt., transition zone, 19-Feb-2006, leg. Ziemmeck 949 (CDS 28857].

Vertiginidae Fitzinger, 1833

Gastrocopta Wollaston, 1878

Gastrocopta sp.

Figures 3A, 5I

Taxonomic comment. The single specimen of this micromollusk found during the survey of herbarium material could only be identified to genus. The material is currently being examined together with several specimens not found to be associated with lichens or bryophytes. It possibly belongs to a new, presently undescribed species.

Distribution. A common genus, recorded on 14 islands (see MIQUEL & HERRERA 2014).

Affinity to lichens and liverworts. Not necessarily closely associated; only once found as a by-catch (on *Brachymenium systylium* from a basalt boulder in transition-zone forest of Pinzón, a habitat not significantly different from other collection sites of the snail).

Specimen examined. Isolated from bryophyte. ICCDRS 40516: 1 specm. from *Brachymenium systylium* [Ecuador: Galapagos. Pinzón: along trail going up from Playa Escondida; 0° 36' 42" S, 90° 40' 27" W, 318 m alt., transition zone, 16-Feb-2006, leg. Ziemmeck 646 (CDS 27385)].

Discussion

Micro-mollusks using Galapagos lichens and bryophytes as their habitat

It is difficult to assess how closely snail specimens found as part of our survey are associated with lichens or bryophytes. The observed associations are not based on a statistical analysis and herbarium specimens were not originally collected with the purpose to detect micromollusks. Instead one can expect that the tiny animals are easily lost as part of the collection routine, when specimens are removed from their original bags, transferred to herbarium packets and, during identification repeatedly taken out of these packets. In this respect it is not surprising that no micro-mollusks were detected among crustose lichens or thallose liverworts. But it is remarkable that these minute animals can regularly be found "trapped" among the structurally more complex foliose and fruticose lichens and bryophytes.

Comparing the species found, Pupisoma galapagorum was the most frequently encountered micro-mollusk. By comparison, finding other snail species appears almost accidental. Clearly, all these species, even Pupisoma, can also be found not associated with lichens and bryophytes (MIQUEL & HERRERA 2014). Particularly interesting is the discovery of Tornatellides chathamensis on a lichen. This snail is known to inhabit fern fronds, a fairly exposed habitat with a less humid, less sheltered micro-climate than leaf-litter on the ground, which most other Galapagos micro-mollusks seem to prefer. Similarly, P. galapagorum has been reported also from finch nests, which is perhaps unsurprising: Darwin's finches (Geospizini) frequently weave lichens into their nests and the outside of these nests is as exposed as the branches inhabited by epiphytic lichens or bryophytes.

The forests where species of lichen and bryophyte inhabited by P. galapagorum were found belong to the transition zone. These sites, though characterized by frequent garúa (a fine drizzle or mist), are not as humid or even rain-drenched as the forests of the humid zone, habitats that are most characteristic of the majority of Galapagos micro-mollusks. Although we specifically surveyed sites where herbarium specimens had originally been collected, the snails found there were not notably more common among lichens or bryophytes; instead most snail species were found on other substrates. However, it is difficult to assess how effective routine collection procedures are in finding these minute organisms. Hiding between structurally complex lichens or bryophytes, animals less than a few millimeters in size will generally be challenging to find if using only a hand lens. Screening with a binocular microscope in the laboratory will certainly yield better results. Thus it is quite possible that in the field these small animals are more easily detected among structurally less complex substrates (leaf litter, wood or rock surfaces, open soil, etc.), particularly if efficient techniques, such as sieving of the substrate, are employed. By contrast, sieving lichen and bryophyte specimens has not proven an efficient method to discover micro-mollusks. Generally the technique did not yield any specimens, perhaps because the animals adhered to the thalli or possibly because they are trapped among the complex microstructures.

Nevertheless, with the exception of *P. galapagorum* and perhaps *T. chathamensis*, most Galapagos micromollusks do not appear to be closely associated with lichens or bryophytes. Only these 2 species seem to be better adapted to drier micro-climates and therefore perhaps more regularly inhabit lichens and bryophytes of the transition zone forests.

Micro-mollusks feeding on Galapagos lichens and bryophytes

Finding lichen material (spores, hyphae, algae) in squash preparations of P. galapagorum isolated from Heterodermia suggests that this lichen is at least occasionally part of the Pupisoma diet. The genus Heterodermia is characterized by brown, one-septate spores, similar to those found inside the digestive tract of the snail (Fig. 1G, H, I). Heterodermia has photobionts that belong to Trebouxia Puym., which is overall the most common alga found in lichens, characterized by a wavy chloroplast, structurally similar to the one observed inside the algae found in the Pupisoma squash (Fig. 1E, F). Algae with an orange color (their green chlorophyll masked by carotenoids) were also observed (Fig. 1G). These may correspond to another common photobiont, Trentepohlia Mart., which is a genus of algae particularly common in tropical lichen species. Hyphae, also detected in the squash (Fig. 1G, I), may have been part of the lichen, but microscopically they cannot be distinguished with certainty from hyphae of non-lichenized fungi.

Lichen residue was not found in the *Pupisoma* squash isolated from *Squamidium nigricans*. Instead a leaf fragment structurally identical to the leaf apex of this moss was observed (Fig. 1D).

Thus, snails isolated from *Heterodermia* contained lichen fragments, the specimen isolated from *Squamidium* material that belonged to this moss — both evidence that *P. galapagorum* not only utilizes these organisms as its habitat but, at least occasionally, also feeds on them. However, with only 3 snail specimens examined, assessing how frequently *Pupisoma* uses lichens or bryophytes as its diet is, at this stage, premature. It is certainly possible that the snail regularly feeds on lichens or bryophytes, but it is equally possible its feeding preferences are opportunistic. Perhaps, after having been collected as a by-catch, before being dried the snail had no option but to feed on the only material available, the herbarium specimens.

Predatory Galapagos micro-mollusks

While the majority of gastropods reported here are herbivores, we were surprised to discover also a new, previously unknown, predatory snail among the herbarium specimens: this species is here newly described as *Scolodonta rinae*.

The micro-morphology of its radula is consistent with other members in the genus and indicates that the species is carnivorous. During our field survey *Scolodonta* could not be re-discovered among lichens or bryophytes, but the immediate vicinities of its collection sites were littered with empty shells of *P. galapagorum*. It seems reasonable to suggest that *Pupisoma*, which regularly inhabits lichens and bryophytes, and probably at least occasionally consumes them as part of its diet, may in turn be eaten by its predator *S. rinae*. This would explain why the carnivorous *S. rinae* was occasionally also found as a by-catch among herbarium specimens.

Whether Scolodonta represents a recent introduction or should be considered an overlooked endemic cannot be answered with certainty. We found the new species in a highly disturbed habitat. The forests around Los Gemelos are among the last fragments of formerly extensive Scalesia pedunculata woodland in the highlands of Santa Cruz. These forests are today strongly invaded by a multitude of introduced species, among them the notorious blackberry (Rubus niveus, which forms a weedy undergrowth that chokes natural forest recovery); highly problematic is also the giant African land snail, Lissachatina fulica (see PARENT et al. 2014: http://darwinfoundation.org/ datazone/checklists/18132/, accessed 6-Sep-2016). If a large snail like Lissachatina can intentionally be introduced despite strict quarantine inspections, it is certainly possible that a predator as minute as Scolodonta has been accidentally introduced unnoticed. The species is the smallest of all terrestrial gastropods now known from Galapagos, and easily overlooked. Even if these forests have, for years, intensively been studied, the micro-mollusks have, until recently, escaped attention (MIQUEL & HERRERA 2014).

Nevertheless, although the area around Los Gemelos is today heavily disturbed, these forests remain the last remnants of an original vegetation that, in the past, might have supported not only herbivorous but also some carnivorous snails. The unusually high abundance of *S. rinae* there (more than half of all micro-mollusks collected) and the abundance of empty *Pupisoma* shells in its immediate vicinity could be interpreted as evidence that *Scolodonta* is indeed, like *Pupisoma*, an endemic relict of these unique forests.

At this stage we clearly do not sufficiently understand ecological interactions of organisms in the Galapagos at this miniature scale. The Galapagos land snails are among the most threatened group of organisms in the archipelago (PARENT 2003, PARENT & SMITH 2006, PARENT & COPPPOIS 2009) and lichenized fungi are one of the most diverse species groups of all Galapagos terrestrial organisms (BUNGARTZ 2016). Both are not the most iconic of the Galapagos species, but studying their ecological interactions should nevertheless be a priority.

Acknowledgements

We thank Henri W. Herrera, the curator of ICCDRS for management of the snail specimens, and Frauke Ziemmeck for managing the cryptogam collection at CDS. Both Henri and Frauke have been extremely helpful, assisting with collecting, data entry, and curation of specimens. We are also much indebted to Xavier Pilataxi, who regularly participated in field surveys and expeditions collecting micro-mollusks and who also assisted with examining and preparing specimens for analysis. We are very grateful to the Charles Darwin Foundation, especially its executive director Arturo Izurieta and science coordinator José Marin, for their continued support of the Galapagos Lichen Inventory. Lenyn Betancourt helped to update specimen records of ICCDRS micromollusks. For research and collection permits we are especially indebted to the staff of the Galapagos National Park, particularly Washington Tapia and Galo Quedaza, and, more recently, Jorge Carrion and Daniel Lara. This publication is contribution number 2154 of the Charles Darwin Foundation for the Galapagos Islands. The Census of Galapagos Biodiversity and the CDF Checklist of Galapagos Species has been supported by several grants to the Charles Darwin Foundation (donors cited at http://www.darwinfoundation.org/datazone/checklists/, accessed 6-Sep-2016). Funding for traveling and SEM analyses was provided by the Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (PIP 2010-0080). The lichen inventory received funds from The Paul and Bay Foundations, and the Erwin Warth Stiftung, the National Science Foundation (projects DEB 0715660 and DEB 0841405). Research with the goal to establish the first IUCN Red List of endemic Galapagos lichens is supported by the Mohamed bin Zayed Species Conservation Fund (project 152510692). We are very grateful to the editor, John Hutchinson, for his extensive comments that considerably improved the manuscript. We would like to thank Liew Thor Seng and a second anonymous reviewer for their constructive criticism.

References

- ADAMS, C.B. (1845) Specierum novarum conchyliorum, in Jamaica repertorum, synopsis. Pars II Species terrestres. *Proceedings of* the Boston Society of Natural History 2: 11–17.
- ANDERSON, R. (1997) Species inventory for Northern Ireland land and freshwater Mollusca. Belfast: Department of the Environment for Northern Ireland, Environment and Heritage Service.
- BAUR, B. & BAUR, A. (1997) *Xanthoria parietina* as a food resource and shelter for the land snail *Balea perversa*. *Lichenologist* **29**: 99–102.
- BREURE, A.S.H. & MIQUEL, S.E. (2012) More than a number: clarifying the dates of publication of some papers of A. Doering on land and freshwater shells from Argentina and a note on his taxon *Clessinia* (Odontostomidae). *Zootaxa* **3572**: 18–22.
- BUNGARTZ, F., ZIEMMECK, F., YÁNEZ-AYABACA, A., NUGRA, F. & APTROOT, A. (2013) CDF checklist of Galapagos lichenized fungi. In: BUNGARTZ, F., HERRERA, H., JARAMILLO, P., TIRADO, N., JIMÉNEZ-UZCÁTEGUI, G., RUIZ, D., GUÉZOU, A. & ZIEM-MECK, F. (Eds) Charles Darwin Foundation Galapagos species checklist. http://www.darwinfoundation.org/datazone/checklists/ true-fungi/lichens/ [last updated 3 December 2013.
- BUNGARTZ, F. (2016) Lichen diversity: unexpected interactions among overlooked blotches and splotches. Pp. 53–59 in: DE Roy, T. (Ed.) Galapagos, preserving Darwin's legacy. 2nd edition. Auckland: Bateman.
- COKER, P.D. (1967) Damage to lichens by gastropods. *Lichenologist* **3**: 428–429.
- DALL, W.H. (1892) On some types new to the fauna of the Galapagos Islands. *Nautilus* 5: 97–99.

- DALL, W.H. & OCHSNER, W.H. (1928) Landshells of the Galapagos Islands. *Proceedings of the California Academy of Sciences* (4th Series) 17: 141–185.
- FRÖBERG, L., BAUR, A. & BAUR, B. (1993) Differential herbivore damage to calcicolous lichens by snails. *Lichenologist* 25: 83–95.
- FRÖBERG, L., BJÖRN, L.O., BAUR, A. & BAUR, B. (2001) Viability of lichen photobionts after passing through the digestive tract of a land snail. *Lichenologist* 33: 543–545.
- GAUSLAA, Y., HOLIEN, H., OHLSON, M. & SOLHØY, T. (2006) Does snail grazing affect growth of the old forest lichen *Lobaria pul*monaria? *Lichenologist* 38: 587–593.
- GRADSTEIN, S.R. & ZIEMMECK, F. (2014) CDF checklist of Galapagos horn- and liverworts. In: BUNGARTZ, F., HERRERA, H., JARAMILLO, P., TIRADO, N., JIMÉNEZ-UZCÁTEGUI, G., RUIZ, D., GUÉZOU, A. & ZIEMMECK, F. (Eds) Charles Darwin Foundation Galapagos species checklist. http://www.darwinfoundation.org/datazone/checklists/bryophytes/anthocerotophyta-hepatophyta/ [last updated 28 January 2014].
- HAUSDORF, B. (2007) Revision of the American Pupisoma species (Gastropoda: Pupilloidea). Journal of Natural History 41: 1481–1511.
- HYLTON SCOTT, M.I. (1945) Fauna malacológica de Tilcara. Revista del Museo de La Plata (Nueva Serie) Zoología 4: 195–211.
- LAWREY, J.D. (1983) Lichen herbivore preference: a test of two hypotheses. *American Journal of Botany* 70: 1188–1194.
- MIQUEL, S.E. & AGUIRRE, M.L. (2011) Taxonomía de los gasterópodos terrestres del Cuaternario de Argentina. *Revista Española de Paleontología* 26: 101–133.
- MIQUEL, S.E. & HERRERA, H.W. (2014) Catalogue of terrestrial gastropods from Galapagos (except Bulimulidae and Succineidae) with description of a new species of *Ambrosiella* Odhner (Achatinellidae) (Mollusca: Gastropoda). *Archiv für Molluskenkunde* 143: 107–133.
- MIQUEL, S.E., TURIENZO, P. & DI IORIO, O. (2015) Gastropod species found in birds' nests from Argentina. *Revista del Museo Argentino de Ciencias Naturales* 17: 87–96.
- OYESIKU, O.O. & OGUNKOLADE, O.R. (2006) The relationship between the Nigerian garden snail *Limicolaria aurora* and the moss *Hyophila crenulata*. *Journal of Bryology* 28: 104–107.
- PARENT, C.E. (2003) Bulimulus (Assessment of 57 Bulimulus land snail species from Galapagos). In: IUCN, (Ed.) IUCN Red List of threatened species. http://www.iucnredlist.org/ [accessed 23 August 2016].
- PARENT, C.E. & COPPOIS, G. (2009) On the snail's trail: Evolution and speciation among a vanishing tribe. In: DE ROY, T. (Ed.) Galapagos, preserving Darwin's legacy. 1st edition. Auckland: Bateman, p. 74–81.
- PARENT, C.E., MIQUEL S.E. & COPPOIS, G. (2014) CDF checklist of Galapagos terrestrial and brackish water snails. In: BUNGARTZ, F., HERRERA, H., JARAMILLO, P., TIRADO, N., JIMÉNEZ-UZCÁTEGUI, G., RUIZ, D., GUÉZOU, A. & ZIEMMECK, F. (Eds) Charles Darwin Foundation Galapagos species checklist. Available from: http:// www.darwinfoundation.org/datazone/checklists/terrestrialinvertebrates/gastropoda/ [last updated 21 May 2014].

- PARENT, C.E. & SMITH, R.P. (2006) Galapagos bulimulids: status report on a devastated fauna. *Tentacle* 14: 25–27.
- PEAKE, J.F. & JAMES, P.W. (1967) Lichens and Mollusca. Lichenologist 3: 425–428.
- PILSBRY, H.A. (1934) [Pupillidae, continued]. Manual of conchology, structural and systematic: with illustrations of the species. Second Series: Pulmonata 28: 97–160, pls 13–23.
- PILSBRY, H.A. (1948) Land Mollusca of North America (north of Mexico), Vol. 2, Part 2. *Monographs of the Academy of Natural Sciences of Philadelphia* 3: i–xlvii + 521–1113.
- PLITT, C.C. (1934) A lichen-eating snail. The Bryologist 37: 93-95.
- Rosso, A.L. & MCCUNE, B. (2003) Exploring the effects of mollusk herbivory on an epiphytic lichen community. *Evansia* 20: 15–21.
- SPESSARD-SCHUETH, L. (1994) Squamidium (C.Müll.) Broth. Pp. 722–725 in: SHARP, A.J., CRUM, H. & ECKEL, P.M. (Eds) The moss flora of Mexico. Vol. 2. Memoirs of the New York Botanical Gardens 69.
- SHACHAK, M., JONES, C.G. & GRANOT, Y. (1987) Herbivory in rocks and the weathering of a desert. *Science* 236: 1098–1099.
- SZLAVECZ, K. (1986) Food selection and nocturnal behavior of the land snail *Monadenia hillebrandi mariposa* A.G. Smith (Pulmonata: Melminthoglyptidae). *Veliger* 29: 183–190.
- VATNE, S., SOLHØY, T., ASPLUND, J. & GAUSLAA, Y. (2010) Grazing damage in the old forest lichen *Lobaria pulmonaria* increases with gastropod abundance in deciduous forests. *Lichenologist* 42: 615–619.
- WIESENBORN, W.D. & GOLDSMITH, S. (2003) White desertsnail, *Eremarionta immaculata* (Gastropoda: Pulmonata), activity during daylight after winter rainfall. *Southwestern Naturalist* 48: 202–207.
- WILLIAMSON, P. & CAMERON, R.A.D. (1976) Natural diets of the landsnail Cepaea nemoralis. Oikos 17: 493–500.
- YOM-TOV, Y. & GALUN, M. (1971) Notes on the feeding habits of the desert snails *Sphincterochila boissieri* Charpentier and *Trochoidea (Xerocrassa) seetzeni* Charpentier. *Veliger* 14: 86–89.
- ZIEMMECK, F. & HARPEL, J. (2014) CDF checklist of Galapagos mosses. In: BUNGARTZ, F., HERRERA, H., JARAMILLO, P., TI-RADO, N., JIMÉNEZ-UZCÁTEGUI, G., RUIZ, D., GUÉZOU, A. & ZIEMMECK, F. (Eds) Charles Darwin Foundation Galapagos species checklist. http://www.darwinfoundation.org/datazone/ checklists/bryophytes/musci/ [last updated 28 January 2014].

Manuscript submitted 6 September 2016 Revised manuscript accepted 11 February 2017