Journal of
Molluscan Studies

The Malacological Society of London

Journal of Molluscan Studies (2020) **0**:1–4. doi:10.1093/mollus/eyaa014
Advance Access Publication Date: 0 2020

RESEARCH NOTE

Use of tree resin as a food source by Galápagos land snails: a novel hypothesis for the fossilization of snails in amber

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Understanding the food preference of organisms is fundamental to ecology and conservation biology. However, data on feeding behaviour are scant for many taxa and especially for invertebrates. Terrestrial molluscs eat vascular plant material, which usually makes up the largest fraction of their diet, followed by lichens, fungi, other invertebrates and soil (Ingram & Peterson, 1947; Pallant, 1969; Cates & Orians, 1975; van der Laan, 1975; Carter, Jeffery & Williamson, 1979; Barker, 1989; Speiser & Rowell-Rahier, 1991; Speiser, 2001). Along with the myriad other vascular plant tissues and substances that typically make up their diet, land snails have been reported to feed on sap (Hotopp, 2005; Dourson & Dourson, 2006).

Sap is the fluid transported in xylem cells or phloem sieve tube elements of vascular plants. When sap becomes exposed on the outside of the plant, it hardens into a more viscous substance called resin. When resin forms (usually from an injury to the plant), arthropods and other invertebrates are often attracted to this new food source (Arillo, 2007). Fresh and sticky resin can accumulate and trap (Ross, 2010; Xing *et al.*, 2019) a diverse range of small organisms, which with the hardening of the resin eventually may be fossilized (Arillo, 2007).

Fossils in amber have contributed significantly to our understanding of the evolution and origins of both vertebrate and invertebrate diversity (Grimaldi, Engel & Nascimbene, 2002; Penney, 2010; Rust *et al.*, 2010; Poinar & Wake, 2015; Xing *et al.*, 2016, 2018; Hirano *et al.*, 2019; Sokol, 2019; Yu *et al.*, 2019; Bullis *et al.*, 2020). The occurrence of land-snail inclusions in Cenozoic Baltic and Dominican ambers has been known for some time (e.g. Poinar & Roth, 1991; Stworzewicz & Pokryszko, 2015; Xing *et al.*, 2019). The discovery and study of fossilized land snails in Burmese amber has a much more recent history, with a number of excellently preserved land-snail fossils having been described over the last 2 yr (Yu, Wang & Pan, 2018; Hirano *et al.*, 2019; Neubauer *et al.*, 2019a; Neubauer, Xing & Jochum, 2019b; Xing *et al.*, 2019; Bullis *et al.*, 2020). These fossils represent a remarkable source of information on the taxonomic diversity and morphology of a tropical forest land-snail fauna from the Mesozoic. Despite research interest in the diversity of this fauna, the more general issue of how snails are trapped in resin and are subsequently preserved in amber has not been investigated.

Based on observations of the land-snail fauna of the Galápagos Islands, Ecuador, we here present a novel hypothesis for the preservation of snails in amber. This fauna consists of about 130 species (121 endemic species) belonging to 12 genera in 10 native families (Miquel & Herrera, 2014; Parent, Miquel & Coppois, 2014; Miquel & Brito, 2019). Of all the animal genera with species endemic to the Galápagos, the land-snail genus *Naesiotus* (Bulimulidae), with over 60 currently recognized endemic species, is the most species-rich (Parent & Crespi, 2006, 2009; Parent, Caccone & Petren, 2008, Parent, Miquel & Coppois, 2014; Kraemer *et al.*, 2019; Phillips *et al.*, 2020). In comparison, the next-most species-rich radiations of Galápagos snails are *Gastrocopta* (seven species; Miquel & Brito, 2019) and *Succinea* (four species; Parent, Miquel & Coppois, 2014), respectively. Some of the snails endemic to the Galápagos are of conservation concern (Parent, Miquel & Coppois, 2014). The IUCN Red List of Threatened Species (www.iucnredlist.org/) presently lists 44 Galápagos *Naesiotus* (formerly *Bulimulus*) species as either data deficient or threatened with extinction (i.e. recognized as vulnerable, endangered or critically endangered; IUCN, 2020). The threat status of other Galápagos land snails has not been evaluated using IUCN Red List categories and criteria. While an understanding of the diet of Galápagos land snails is likely to be important in conservation efforts and could inform our understanding of the evolutionary diversification of this group, the position of land snails within the Galápagos food web is not well studied.

On 17 June 2019, on San Cristóbal Island, we found eight species of land snails on and in the resin of the non-native tree species Spanish cedar (*Cedrela odorata*). The snails were observed up to a height of 3.5 m on the trunks of trees (Fig. 1A–C; Table 1). Some individuals were still alive but had difficulty moving (Fig. 1D). Multiple individuals of *Naesiotus bauri*, *N. nuciformis*, *Subulina octona* and *Zonitoides arboreus* were observed eating the resin (Fig. 1E). The same species of snails were found at the same locality in the immediate vicinity of the trees showing resin secretions and oozing (i.e. on the ground, under leaf litter and rocks). Most snails preserved in amber seem to belong to ground-dwelling taxa (Poinar & Roth, 1991; Stworzewicz & Pokryszko, 2015; Yu *et al.*, 2018; Hirano *et al.*, 2019; Neubauer *et al.*, 2019a, b; Xing *et al.*, 2019; Bullis *et al.*, 2020). However, some of these species are small (e.g. Hirano *et al.*, 2019: mean

Figure 1. Galápagos land snails that we observed trapped in and, in some cases, feeding on the resin of *Cedrela odorata*. Arrows indicate snails (**A**) or the shell epiphragm (**D**). **A.** The four species *Naesiotus bauri*, *Tornatellides chathamensis*, *Subulina octona* and the euconulid sp. **B.** *Zonitoides arboreus*. **C.** *Succinea* sp. **D.** Live *N. bauri* trapped in the resin. **E.** *Naesiotus nuciformis* feeding on resin. Scale bars: **A**, 10 mm; **C**–**E**, 5 mm.

Table 1. List of land snails on and in the resin of Spanish cedar (*Cedrela odorata*) on San Cristóbal Island.

Family	Species	Distributional status	Habitat ecology	Behaviour in/on resin
Helicinidae	*Helicina* sp.	Native	Ground dwelling, semi-arboreal, arboreal	Trapped
Bulimulidae	*Naesiotus bauri*	Native	Ground dwelling	Trapped, feeding
	N. nuciformis	Native	Ground dwelling, semi-arboreal	Trapped, feeding
Achatinellidae	*Tornatellides chathamensis*	Native	Ground dwelling, semi-arboreal, arboreal	Trapped
Achatinidae	*Subulina octona*	Introduced	Ground dwelling	Trapped, feeding
Succineidae	*Succinea* sp.	Native	Ground dwelling, semi-arboreal	Trapped
Gastrodontidae	*Zonitoides arboreus*	Native	Ground dwelling	Trapped, feeding
Euconulidae	Euconulid sp.	Native	Ground dwelling, semi-arboreal, arboreal	Trapped

maximum shell dimension of nine species was *c.* 5.2 mm), and given that smaller individuals are less affected by gravity than larger ones (Noshita, Asami & Ubukata, 2012), it is possible that at least some of these small-shelled species may have been partly arboreal.

Arthropods are sometimes attracted by chemicals present in resin and by other invertebrates (i.e. potential food) trapped in resin (Solórzano Kraemer *et al.*, 2018). Although other animal taxa (e.g. isopods) were trapped in the resin secretions examined by us on San Cristóbal, no snails were observed feeding on these animals. This suggests that at least in this case the snails were attracted to the resin as a potential food source due to odour of chemicals present in the resin (Chase & Croll, 1981). Therefore, we hypothesize that these snails were attracted to some substance in the resin. The land-snail species observed feeding on resin included arboreal and semi-arboreal snails, as well as ground-dwelling snails such as *N. bauri* and *S. octona* (Fig. 1E). At least for the ground-dwelling species, this suggests a specific preference for resin rather than just an accidental or opportunistic encounter. These species had access to other food sources, such as an ample supply of leave litter (e.g. individuals of *N. bauri* were observed eating dead leaves; T. Hirano, personal observation), so were clearly not feeding on resin due to a lack of other options. Although the nutritional requirements of land snails are poorly understood (Speiser, 2001), the snails we found might have been using the resin as a source of calcium carbonate. It is unclear at present, however, whether *C. odorata* has a higher calcium content or nutritional value than other plant species present at the study sites.

The snails we observed trapped in and, in some cases, feeding on the resin included species from six of the ten land-snail families native to the Galápagos (Fig. 1; Table 1). The non-native *S. octona* (Achatinidae), which was most likely introduced from continental South America or the Caribbean (Haas, 1962; Parent, Miquel & Coppois, 2014), was also found in the resin; we note here that one species of fossil achatinids has been reported from Burmese amber (Ross, 2018). *Cedrela odorata* has a similar geographical origin to *S. octona*, having been introduced from Central America and the Caribbean for construction, furniture and shipbuilding (Orwa *et al.*, 2009; Fitter, Fitter & Hosking, 2016; *c.* 1950, Tye, 2001). While the frequency and cause of injuries leading to resin secretions in *C. odorata* are unclear, at our study site the exudation of resin in this tree appeared to be common. Although the resin of *C. odorata* has become part of the diet of endemic Galápagos snails only recently, our observations raise the possibility that land snails may often feed on resin; this would be especially the case if resin represents a source of nutrients that is exuded by trees frequently and in large quantities. The palatability and availability of almost any given food, as well as the nutritional needs of gastropod species, may be subject to seasonal changes, so snail diets may vary greatly over the season (Speiser, 2001). *Cedrela odorata* may have had an impact on the evolution of land-snail behaviour and diet in the Galápagos over the past 50 years, but the nature of this impact is unknown. We also do not know how this exotic tree species compares with native plant species in terms of its nutritive value. The ecological and evolutionary impacts of introduced species on the diet and feeding behaviour of the endemic Galápagos fauna are poorly studied (but see Hendry *et al.*, 2006) and merit more attention.

Resin may collect inside the crevices and openings of trees, as well as dripping off branches or flowing along the outer bark (Xing *et al.*, 2019). Our findings suggest that when resin is available, land snails may feed on it, and that this behaviour in turn may contribute to some individuals being trapped in the resin and ultimately being fossilized in amber (Fig. 1). Published studies and our own observations indicate that land snails might become trapped in resin very quickly (Hirano *et al.*, 2019; Xing *et al.*, 2019). Trapped animals that are struggling to escape could alter resin flows when they are finally fossilized (Arillo, 2007). Xing *et al.* (2019) have suggested that when a snail is trapped in resin, the resin initially flows around the shell of the snail, thus preventing the snail from retracting its body into the shell. However, we did not observe snails crawling in or on the resin with their bodies extended. Therefore, land snails might be able to retract their soft body into the shell even when trapped in resin.

Our results suggest that the Galápagos land-snail fauna can serve as a model to understand how snails are fossilized in resin. Further quantitative studies are needed to clarify the properties making resin a suitable food source for land snails and how the taphonomic process might be influenced by resin.

ACKNOWLEDGEMENTS

This study was supported by a National Science Foundation (NSF) Research Experiences for Undergraduates (REU) site award (no. 1460696), an NSF CAREER award (no. 1751157) to C.E. Parent and an Overseas Research Fellowship from the Japan Society for the Promotion of Science (JSPS) to T. Hirano (no. 201860309). J.G. Phillips and C.E. Parent also received funding (grant no. 897809) from the NSF-funded BEACON Center for the Study of Evolution in Action (DBI-0939454). The Galápagos National Park Directorate provided permits (GNDP permit no. PC-63-19) and invaluable logistic help that made this work possible. Finally, we thank D. Raheem, S. Schneider and an anonymous referee for providing valuable comments and suggestions on earlier drafts of the manuscript.

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