

Research Article

New records of *Otala lactea* (Müller, 1774) and *Zachrysia provisorica* (Pfeiffer, 1858) in Hawaii: using collaborative networks to combat invasive sleeper populations

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Abstract

Hawaii, despite being only about 0.2% of the land mass of the continental United States, accounts for nearly half of all endangered species listed under the Endangered Species Act. Among the most prominent threats to biodiversity, including climate change and habitat destruction, impacts from invasive species are among the most notable. Each year dozens of novel plant and animal species are introduced and establish in Hawaii, and it is likely that many more go undetected. Those that establish and spread negatively impact the nearly 10,000 endemic species that evolved in isolation over millions of years. This process of rapid extinction of native species and replacement with globally distributed generalists is homogenizing Hawaii's unique fauna, causing the islands' biota to resemble more and more that of any other warm rocks in the ocean. The loss of biodiversity extends beyond species loss, and with each extinction, we are losing the stories and connections we have with the land through our shared evolutionary history, connections on which the hope to preserve the distinctive culture and ways of living in Hawaii, and globally, depend. Here we report the case of two newly recorded invasive snail species, *Otala lactea* and *Zachrysia provisorica*, and emphasize the necessity of formalizing and broadening partnerships to help stem the tide of invasive species and help conserve the valuable natural and biocultural resources on which island life relies. Hawaii, like many oceanic islands, serves as a microcosm for processes impacting the entire world. The lessons learned, and practices applied here can help develop prevention and management policies and actions that can be scaled up to stem biodiversity loss globally.

Key words: invasive species, sleeper populations, taxonomy, nursery, early detection

Introduction

The rate of human-mediated species introductions has been increasing steadily in the last two centuries and shows no sign of slowing (Seebens et al. 2017). The ongoing biotic homogenization that is characteristic of the Anthropocene is having disastrous impacts to ecosystem stability and functions (Wang et al. 2021; Cowie et al. 2022). Early detection of non-

native species provides the best chance of controlling them before they become invasive and overrun an ecosystem, resulting in severe ecological and economic damage (Alvarez and Solis 2018; Larson et al. 2020). Yet, most invasive species, particularly members of poorly studied invertebrate groups, persist as sleeper populations (established but undetected) long before the first reports of environmental impacts (Walsh et al. 2016; Spear et al. 2021). Keys to prevention, early detection, rapid response, and effective mitigation include the development of collaborative networks, adequate agency staffing, and proper training for those entities tasked with biosecurity and resource management (Büyüktaktin and Haight 2018; Rabaglia et al. 2019; Diagne et al. 2020; Reaser et al. 2020). Financial and infrastructural support for partnerships among government, non-governmental, private agencies, and those organizations that harbor the taxonomic expertise and experience necessary to survey for and identify novel invaders is needed to develop early detection and rapid responses (Lyal and Miller 2019; Reaser et al. 2020). Outreach and education are needed to engage citizen science efforts to increase capacity for early detection of novel invaders (Vendetti et al. 2018, 2019; Pinkerton et al. 2019).

Natural history museums, which have a long history of documenting and studying biodiversity, make ideal partners for governmental, non-governmental, and private organizations with responsibilities related to biosecurity and management of natural resources (Marsico et al. 2010; Schindel and Cook 2018; Shultz et al. 2021). Additionally, museums are well positioned to lead citizen science initiatives (e.g., SLIME; Vendetti et al. 2018, 2019) that can help fill the gaps left by agencies that are understaffed and underfunded. Although not always formally recognized by the agencies or the museum, malacologists at the Bernice Pauahi Bishop Museum (BPBM) in Honolulu have actively worked to establish such partnerships with the Hawaii Department of Agriculture (HDOA), Hawaii Department of Land and Natural Resources (DLNR), The Nature Conservancy, the Hawaii Invasive Species Council, and many other groups tasked with securing the Islands' valuable natural resources. Most recently, this informal, broad collaborative effort has allowed the early detection and identification of two notorious snail pests introduced to Hawaii.

We report here recent introductions and historical records of two large non-native helicoid land snails in Hawaii, both of which are considered major agricultural pests, and have the potential to impact natural resources and human health in the islands once they become established and spread.

Materials and methods

Snail surveys

Reports of snail interceptions and requests for identifications were brought to the attention of the Malacology staff at BPBM and prompted surveys for

newly introduced species. All surveys for snails were carried out by at least two experienced snail researchers following visual search protocols described in Cowie et al. (2008) for nurseries and by Durkan et al. (2013) in residential and surrounding areas. Snail identifications were done via an integrative approach using conchology, reproductive anatomy, and DNA barcode analyses. To better understand the potential pathways of introductions, additional specimens of each species were also provided by colleagues from other areas in the continental US where they have become established, specifically California and Florida.

Specimen processing

All live collected specimens were killed via the heat shock method of Fukuda et al. (2008) and fixed in 95% ethanol for 24 hours. After 24 hours the bodies were pulled from the shells, a piece of foot tissue removed with a sterile razor and preserved in 95% ethanol for DNA extraction, and the body preserved in 80% ethanol for dissection.

Conchology

Shells were imaged with a digital single-lens reflex camera (Canon EOS Rebel T5i with a 100 mm macro lens) in standard views (aperture, apical, and umbilical). Specimens from this study were used for comparisons with original descriptions and specimens from other collections to verify identifications.

Reproductive anatomy

Two adult specimens (bearing a reflected lip) from each species were dissected with the aid of a Leica M125 stereo scope, and reproductive anatomy photographed using an attached View4K digital camera (I. Miller Microscopes, PA). Multiple images were stitched together to form one composite image in Photoshop (CC) and then enhanced for contrast. Figures of shells and anatomy were produced using Adobe Illustrator (CC).

DNA extraction, amplification, and sequencing

Genomic DNA (gDNA) was extracted from an approximately 3 mm³ piece of preserved foot tissue using the Macherey-Nagel NucleoSpin® Tissue Kit following the manufacturer's instructions. Tissue samples and gDNA were cryopreserved in the Pacific Center for Molecular Biodiversity (PCMB) at BPBM (PCMB 50500-01, 50753, 52264-65, 52281, 55101-02, 60874-78). A portion of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified via the polymerase chain reaction (PCR) using primers LCO1490/HCO2198 (Folmer et al. 1994). Reactions were carried out in 25 µl volumes containing 1–2 µl template DNA and a final concentration of 1 U of MangoTaq™ DNA polymerase (Bioline), 1X reaction buffer, 0.2 mM

each dNTP, 2.5 mM MgCl₂, 0.75 μM of each primer, 0.4 μg/μl BSA, and 0.5% DMSO. Cycling parameters consisted of a single cycle of 5 min at 95 °C, 1 min at 45 °C, 1 min at 72 °C, followed by 34 cycles of 95 °C, 48 °C, and 72 °C for 30 s each, and a final extension of 5 min at 72 °C. A final 4 °C incubation of 10 min terminated each reaction. The amount and specificity of amplifications were verified via agarose gel electrophoresis and single product amplicons were cycle sequenced using an ABI BigDye terminator kit (Perkin-Elmer Applied Biosystems, Inc., Waltham, Massachusetts). Sequences were electrophoresed and analyzed on an ABI 3730XL (Perkin-Elmer Applied Biosystems, Inc.) at Eurofins Genomics, LLC (Louisville, Kentucky). All loci were initially sequenced in one direction, and all unique haplotypes sequenced in the other direction to produce full contigs. All sequences have been uploaded to the Barcode of Life Database (BOLD) and to GenBank (Accession numbers: OP898289–OP898303).

Electropherograms were checked for errors, edited and assembled using Geneious Prime 2020.2.2 (<http://www.geneious.com>). Sequences of COI generated as part of this study and publicly available sequences downloaded from Genbank were unambiguously aligned using MAFFT ver. 7.388 with the iterative refinement method E-INS-I (Kato and Standley 2013) implemented in Geneious Prime. Alignments were checked against amino acid sequences as references to verify an open reading frame and then exported in FASTA format for subsequent phylogenetic analyses.

Barcoding and phylogenetic reconstruction

To corroborate species identifications, COI sequences were compared with other barcodes on BOLD via the Identification Engine System. Phylogenetic reconstruction was conducted under the minimum evolution inference using K2P distances and 500 bootstrap replicates implemented in MEGAX ver. 10.2.2 (Kumar et al. 2018). Trees produced in MEGA were exported as images and edited for publication in Adobe Illustrator.

Results

Surveys prompted by quarantine interceptions and reports of invasive species by citizens of Oahu resulted in two new state records for Hawaii. Conchology, reproductive anatomy, and phylogenetic analyses confirm the identities of these two newly introduced species in Hawaii as *Otala lactea* (Müller, 1774; Figure 1) and *Zachrysia provisoria* (Pfeiffer, 1858; Figure 2).

The dark-chocolate brown aperture and parietal callus of the *O. lactea* shells were consistent with this species. The shell and anatomy (Figure 3) of specimens collected on Oahu were also consistent with specimens collected in Los Angeles County, California, and with descriptions of this species by Schileyko (2006).

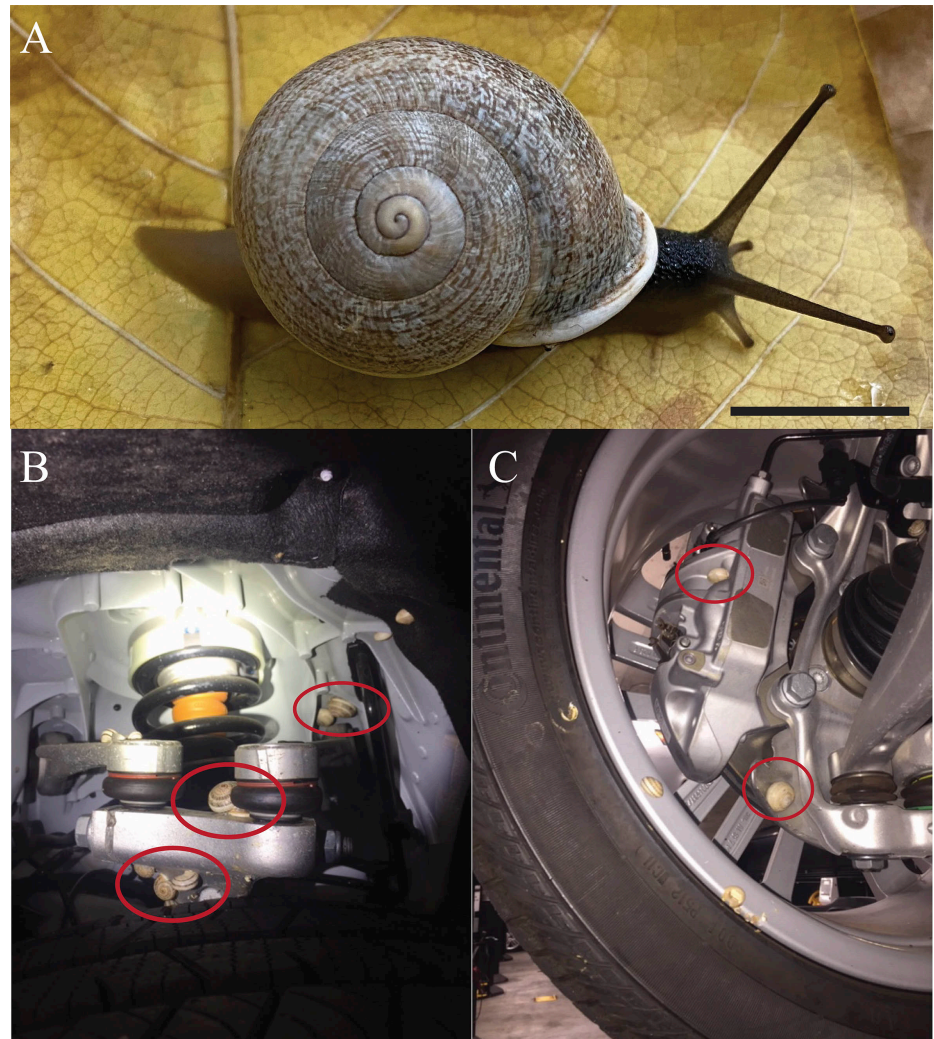


Figure 1. A) Live *Otala lactea* collected from Ford Island, Oahu residence. Scale Bar = 1 cm. B–C) Wheel well and wheel of imported car showing a few of the estivating *Otala lactea* (red circles). Photo credits: T.M.B. Maruno (A) and Hawaii Department of Agriculture (B–C).

The shells of *Z. provisoria* specimens were consistent with those identified as such in other collections, and consistent with previous descriptions (Pilsbry 1889; Schileyko 2006). Anatomically, the possession of a large phallus, a long flagellum, and an accessory flagellum is consistent with this species (Figure 4; Schileyko 2006).

The 655 bp sequences from three specimens of *O. lactea* from Oahu produced two COI haplotypes that differed by less than 2.5%. One of these (PCMB52281) from a Ford Island residence was sister to the other (PCMB50500), which was recovered in a strongly supported clade of sequences from specimens collected in Los Angeles, CA (PCMB60874-60876; Figure 5). All these newly sequenced specimens were nested within a strongly supported clade with several other *O. lactea* from the Iberian Peninsula (Portugal and Spain) uploaded to Genbank.

Sequences from five specimens of *Z. provisoria* from Oahu and one specimen from Fort Lauderdale, Florida produced a single COI haplotype, which was 100% identical to two sequences deposited in BOLD, one of which



Figure 2. A) Live *Zachrysia provisorio* collected from Kaneohe, Oahu residence. Scale bar = 1 cm. B–C) Garden planters and cinder block where snails were estivating. Scale bar = 1 cm. Photo credits: T.M.B. Maruno (A) and K.A. Hayes (B–C).

was collected in Key Largo, Florida and the other unknown due to the data being unpublished and set to private on BOLD. A third sequence of *Z. provisorio* on BOLD was 99.69% similar to the specimens from Oahu. Phylogenetic analyses recovered the Hawaii, Florida, and BOLD specimens in a single, strongly supported clade (Figure 6) sister to the Rhytididae, *Afrohytida krausii* (Pfeiffer, 1846), listed under *Natalina kraussi* on GenBank (FJ262298.1). The sister relationship of the latter is unsupported in the tree.

Helicidae

***Otala lactea* (O.F. Müller, 1774) New State Record**

Otala lactea is a large (shell diameter ≤ 36 mm), polyphagous, land snail native to the lands bordering the western Mediterranean Sea (Pilsbry 1939;

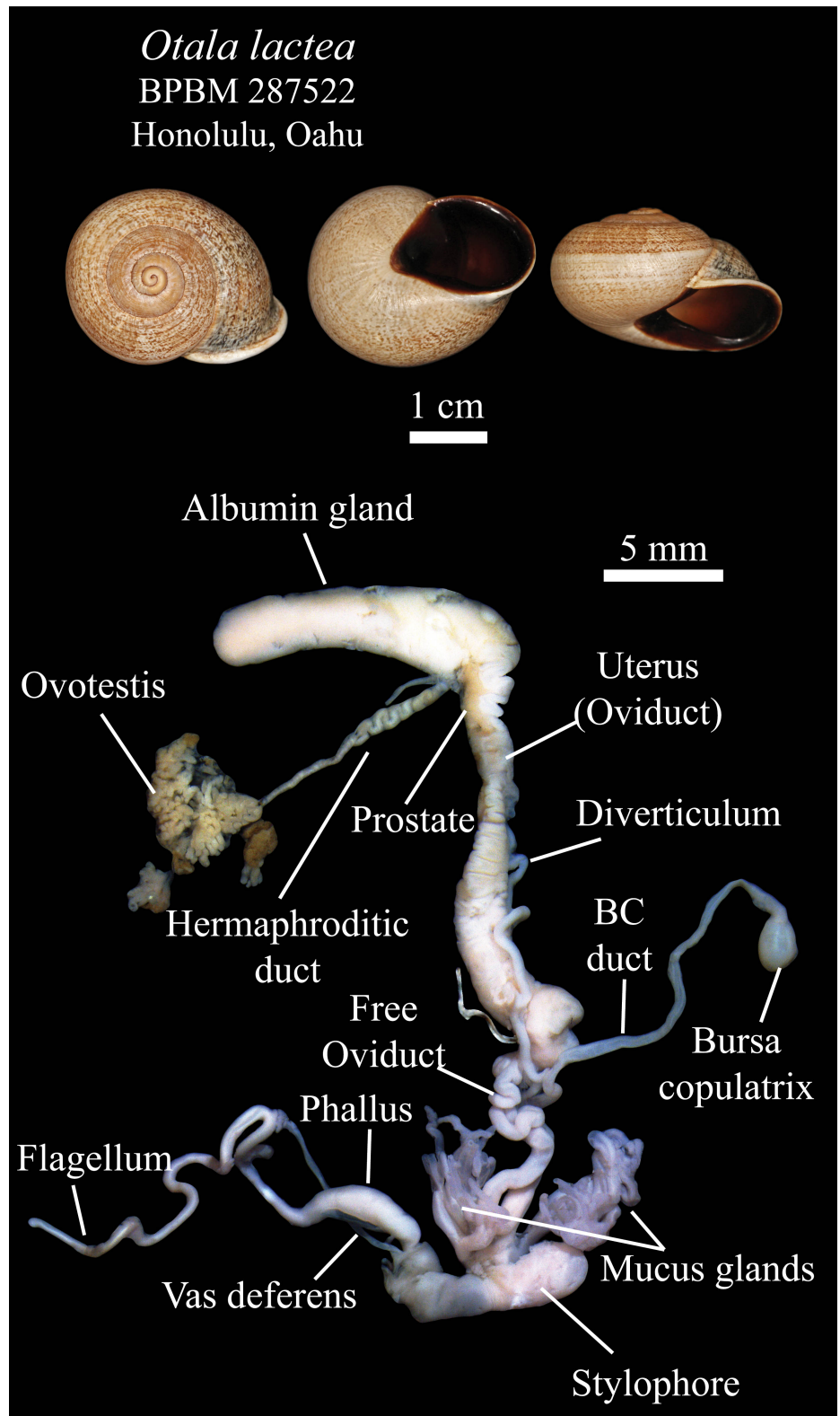


Figure 3. *Otala lactea* shell (top) and reproductive anatomy (bottom). BC = Bursa copulatrix. Photo credits: T.M.B. Maruno (shell) and K.A. Hayes (reproductive anatomy).

USDA-APHIS 1999; Bank and Neubert 2017; Holyoak and Holyoak 2017). Its status as native to that region is evidenced by its lengthy archaeological record in Spain (Serrano et al. 1997; Cortéz-Sánchez et al. 2008, 2019, 2020; García-Rivero et al. 2019), Morocco (Ramos et al. 2011; Limondin-Lozouet

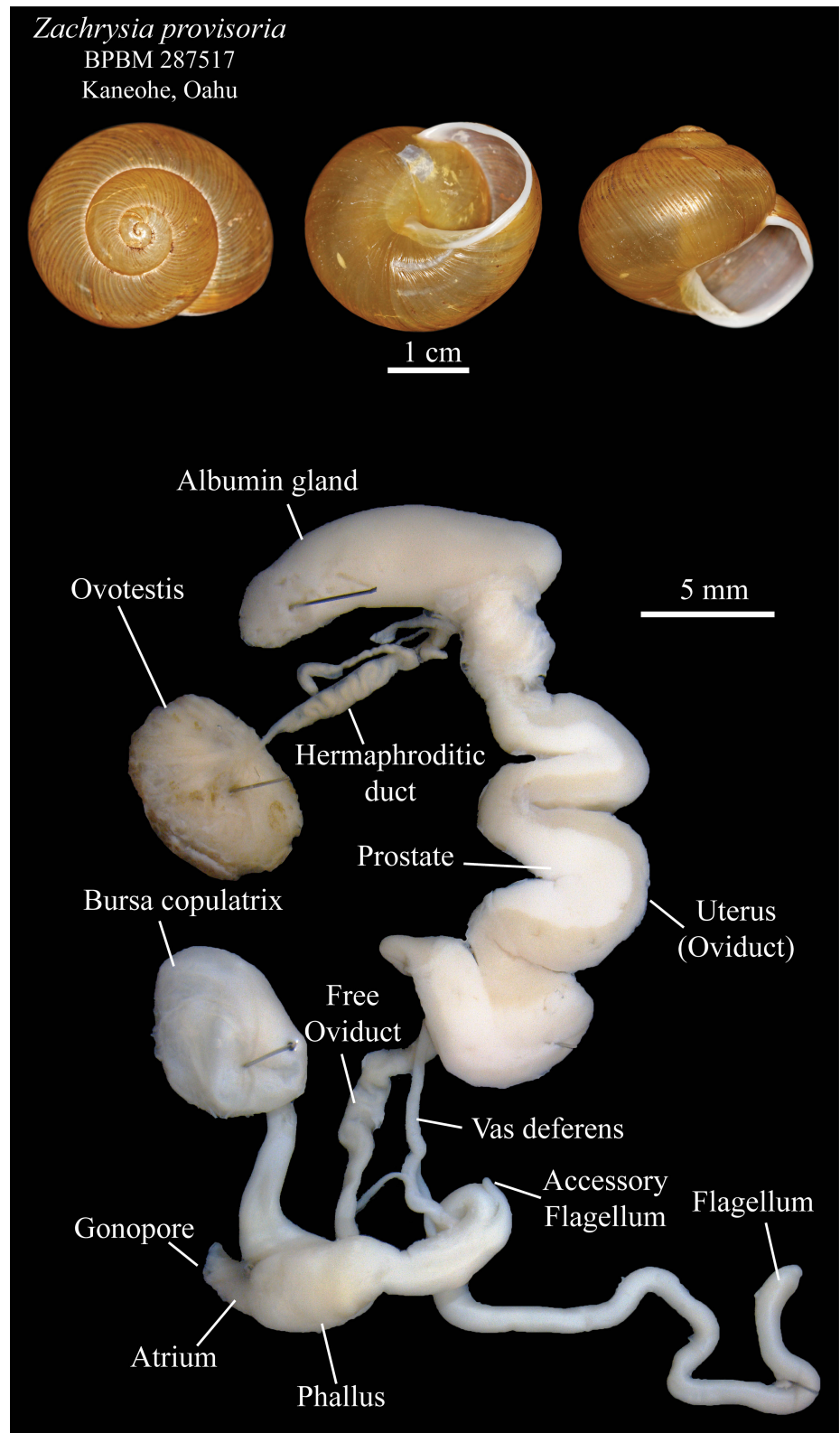


Figure 4. *Zachrysis provisorio* shell (top) and reproductive anatomy (bottom). Photo credits: T.M.B. Maruno (shell) and K.A. Hayes (reproductive anatomy).

et al. 2013; Hutterer et al. 2014), Algeria (Chellat et al. 2018), and Tunisia (Saafi et al. 2013). The species occurs in the Balearic Islands (Beckmann 2007), but its status as native or introduced is ambiguous; Rosselló and Cuerda (1973) reported fossil molds of shells identified as this species from

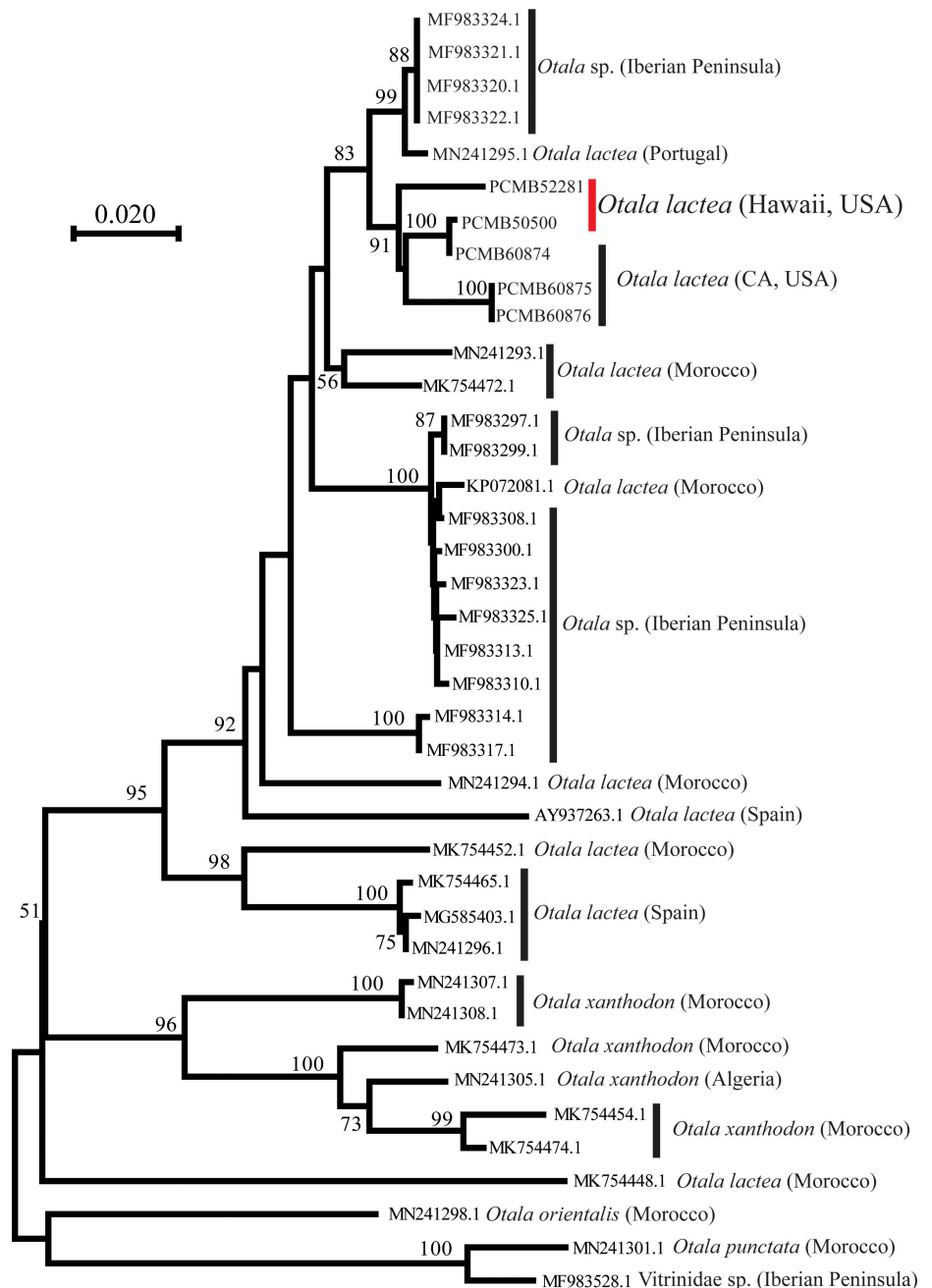


Figure 5. Phylogenetic reconstruction using minimum evolution of COI sequences of select *Otala* species downloaded from Genbank and *Otala lactea* sequenced for this study. OTUs for Genbank sequences labeled according to identifications and localities provided with Accession data. Node values are bootstrap supports from 500 replicates.

Mallorca. Mercadel et al. (1970) reported Quaternary fossils of this species from the island of Menorca, but subsequent authors have cast doubt on the validity of that record, suggesting that the species is instead an anthropogenic introduction (Paul 1984; Quintana 2001, 2006; Vicens and Pons 2011, 2017). If so, the introduction was of considerable antiquity, as the species was present in Roman times (Jaume et al. 2011). It also occurs in mainland Portugal, Madeira, the Azores, and the Canary and Cape Verde Islands (Backhuys 1975; Groh 1983, 1985; Abreau 1998; Seddon 2008; Cameron et al. 2012; Cadevall and Orozco 2016; Bank and Neubert 2017; Holyoak et al.

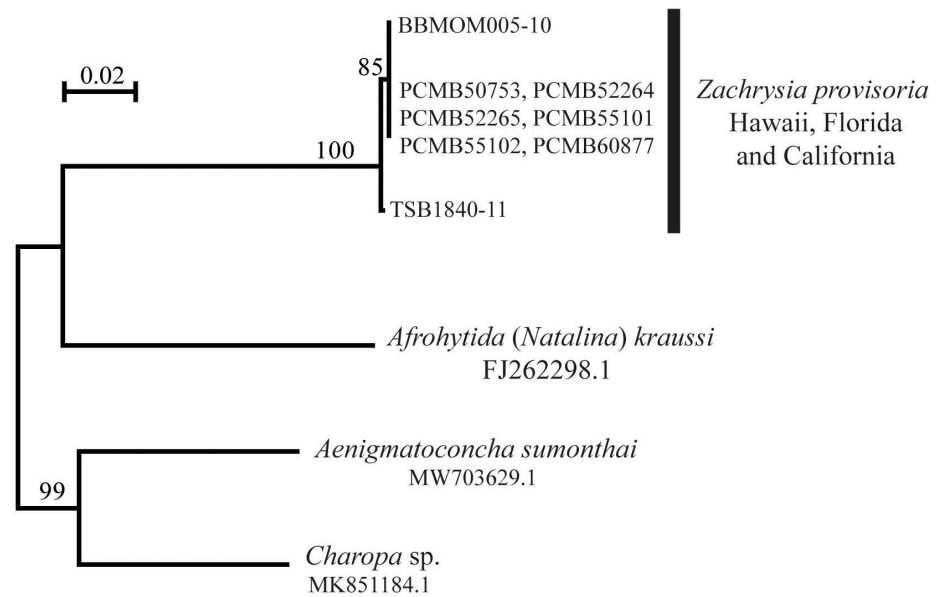


Figure 6. Phylogenetic reconstruction using minimum evolution of COI sequences of select *Zachrysia provisoria* downloaded from BOLD, outgroup taxa from Genbank, and *Z. provisoria* sequenced for this study. OTUs for downloaded sequences are labeled according to identifications provided in BOLD and Genbank. Node values are bootstrap supports from 500 replicates.

2019). The species has been reported to occur in Malta (Mifsud et al. 2003), but Cilia (2012) suggests that Mifsud's material may instead have been misidentified specimens of *Otala punctata* (Müller, 1774), known to occur on the island (Barbara and Schembri 2008).

The range of *O. lactea* has been substantially expanded because of human commerce, and the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA-APHIS) considers *O. lactea* a quarantine-significant pest (a pest of potential economic importance to the area, which, if intercepted, requires phytosanitary action) for Hawaii, Puerto Rico, and the US Virgin Islands under the federally recognized state managed phytosanitary program. The species is a favored food item among the peoples of its Mediterranean homeland, and its spread is believed to have been at least in part the result of intentional introductions by persons wishing to use it for that purpose (Gammon 1943; Grimm 1964; Hanna 1966). It became established in Uruguay early in the 19th century (d'Orbigny 1835; Rush 1892; Campos and Calvo 2006). Elsewhere in South America, it now occurs in Argentina (Rush 1892; Rumi et al. 2010), Chile (Rumi et al. 2010; Araya 2015), and Paraguay (Rumi et al. 2010). Mienis (2001) contended, however, that all records of *O. lactea* from Uruguay and probably also Argentina, are in fact misidentifications of *O. punctata*. Although *O. lactea* has not been recorded within Mexico, specimens have been intercepted by US agricultural inspectors in shipments of goods entering the US from Mexico (Naranjo-García and Castillo-Rodríguez 2017), for example from Tamaulipas (USDA APHIS interception). It has been reported to occur in Cuba (Tryon 1888; van der Schalie 1938; USDA-APHIS 1999), but although the living individuals have been imported to Cuba for gastronomic purposes

it is not believed to have become established there (Aguayo 1944; Maciera et al. 2013).

Accurate determination of first records and the spread in the US is complicated by taxonomic confusion. Say (1822) described a species he named *Helix irrorata* based on specimens said to have been collected in Pennsylvania; in the description he compared it with *lactea*. Binney (1885: 249–251), in a discussion of “doubtful, spurious, extralimital, species of *Helix*,” stated that Say’s *irrorata* was a synonym of *lactea* and that the species “[d]oes not now exist in America.” The earliest confirmed report of its subsequent reestablishment in the United States is that of Strecker (1935) in Texas; there are numerous subsequent Texas records (Jackson 1944; Grimm 1964; Pratt 1964; Murray 1968; Mead 1971). *Otala lactea* has also been reported to occur in California (Hill 1941; Gammon 1943; Grimm 1964; Hanna 1966; Roth and Sadeghian 2006), Arizona (Mead 1971; Bequaert and Miller 1973), Mississippi (Hubricht 1963; Mead 1971), Kentucky (Mead 1971), Virginia (Grimm 1964; Mead 1971), Georgia (van der Schalie 1938; Pilsbry 1939; Mead 1971; Felix et al. 2019), and Florida (Henderson 1936; van der Schalie 1938; Pilsbry 1939). It has also been reported from Louisiana, but apparently did not become established (Harry 1948; Dundee and Watt 1961). USDA-APHIS (1999) suggests, however, that some of the early records may be misidentifications of *O. punctata*.

In addition to the above North and South American localities, *O. lactea* has become established in Bermuda (Gould 1969; Doleman 1973; Bieler and Slapcinsky 2000) and in Australia (Burch 1976; Smith 1992; Blacket et al. 2016). Melvill and Ponsonby (1898) and Connolly (1939) cited an early collection of this species in South Africa, but Herbert and Sirgel (2001) and Herbert (2010) stated that the species had not become established and suggested that at least some of the South African reports of this species were based on misidentifications of the similar species *O. punctata*.

Otala lactea feeds on a variety of agricultural and horticultural plants and is a common garden pest in many areas where it is established (USDA-APHIS 1999). In Florida it causes only minor damage (Capinera and White 2011) and has been described as a “minor plant pest” (Cowie et al. 2009), though in California it does cause damage to commercial crops and home gardens (Gammon 1943). In Bermuda its presence, together with *Rumina decollata* (Linnaeus, 1758), was regarded as a sufficiently significant threat as to justify the introduction of the predatory snail *Euglandina rosea* (Férussac, 1821) as a potential (but unsuccessful) biological control agent (Simmonds and Hughes 1963; Civeyrel and Simberloff 1996). In laboratory experiments *O. lactea* has been found to be a suitable host for *Angiostrongylus cantonensis* (Jindrak et al. 1977). In its native range, *O. lactea* serves as an intermediate host for other protostrongylid nematode parasites of sheep and goats (Cabaret 1979, 1988; Cabaret et al. 1980; Berrag and Urquhart 1996).

The first record of *O. lactea* in Hawaii was from September 3, 1957, when a single, live specimen was found on the deck of the SS *Steel King* by agricultural inspectors on the island of Kauai. In August 2019 HDOA reported finding dozens of live *O. lactea* on a sport utility vehicle (SUV) imported to a local dealership through the Port of San Diego, California (Figure 1) where the SUV was staged prior to shipping. The snails were found estivating in wheel wells and the undercarriage of the SUV (Figure 1). Specimens collected off the SUV by HDOA were provided to malacology researchers at the University of Hawaii and BPBM for identification.

Just over a year later in October 2020, a resident on Ford Island, Oahu, brought a single live snail to researchers at BPBM. The snail was found in the yard of the residence, and a subsequent search of the residence and surrounding area by researchers from BPBM did not recover any additional *O. lactea* specimens.

At this time *O. lactea* is not considered established, as no additional specimens have been reported. However, no systematic surveys are being conducted beyond those reported here. As such, it is possible that *O. lactea* currently exists on Oahu or one of the other islands in sleeper populations.

Material examined

USA – Hawaii, Kauai County, Kauai • 1; Lihue; 13 Sep. 1957; Yoshio Kondo leg.; agricultural intercept on board S.S. *Steel King* vessel; BPBM 279759. – Hawaii, Honolulu County, Oahu • 1; Pearl Harbor; 2 Oct. 2020; Chelsea Colden leg.; BPBM 287522 • 8; Honolulu; 17 Aug. 2019; Janis N. Matsunaga leg.; HDOA interception on an SUV imported via California; BPBM 289115. – California, Los Angeles County • 25; 23 May 2018; Greg Bartman leg.; USDA-APHIS interception; BPBM 289148.

Zachrysiidae

***Zachrysia provisoria* (L. Pfeiffer, 1858) New State Record**

Zachrysia provisoria is a large, phytophagous land snail (shell width ≤ 32 mm) native to Cuba (Pilsbry 1928; Pérez and Espinoza 1993; Espinosa and Ortea 1999). It was intentionally introduced to the United States in the early 20th century by a shell collector in Little River, Florida (Clapp 1919) and is now well established in Florida (Clarke 1957; Clench 1959, 1960; Auffenberg and Stange 1993; Robinson and Fields 2004; Auffenberg et al. 2011). It has since spread more widely in the US and to multiple islands of the Caribbean and Atlantic. It has been reported in the Cayman Islands (Robinson and Fields 2004; Breure et al. 2016), Jamaica (Robinson and Fields 2004; Rosenberg and Muratov 2006; Breure et al. 2016), Hispaniola (Republica Dominicana, Ministerio de Medio Ambiente 2012; Agudo-Padron 2020; Espinosa and Robinson 2021), the Virgin Islands (Auffenberg and Stange 1993; Robinson and Fields 2004; Breure et al. 2016), Anguilla (Breure et al. 2016), Saint

Martin (Bertrand 2001; Breure et al. 2016; Neckheim and Hovestadt 2016; Hovestadt and Neckheim 2020), St. Barthélemy (Breure et al. 2016; Hovestadt and Neckheim 2020), Saba (van Leeuwen et al. 2015), Saint Kitts (Breure et al. 2016), Nevis (Robinson and Fields 2004; Breure et al. 2016), Antigua (Robinson and Fields 2004; Breure et al. 2016), and Guadeloupe (Massemin and Pointier 2010; Breure et al. 2016; Charles 2016). In the Windward Islands it occurs in Barbados (Chase and Robinson 2001; Robinson and Fields 2004; Breure et al. 2016) and Mustique (Robinson and Fields 2004; Breure et al. 2016). It also occurs in Curaçao (van Buurt 2016; Breure et al. 2016; Hovestadt and van Leeuwen 2017) and the Bahamas (Bland 1862; Bendall 1895; Clench 1938; Jacobson 1965; Deisler and Abbott 1984). In addition to the above, snails have been intercepted by quarantine inspectors in shipments to the US from Costa Rica and Guatemala (Robinson and Fields 2004). Beyond the Americas, the species has been reported to be a pest of mulberry in India (Pandey and Dhar 2013).

Zachrysia provisoria is a voracious herbivore reportedly capable of damaging a long list of horticultural and agricultural plants, including fruits and cut flowers (Robinson and Fields 2004; Capinera and White 2011; Aufferberg et al. 2011; Capinera 2013). Impacts on nursery plants can be severe without molluscicide control and in some instances have been estimated to reduce stocks by as much as 25% (Robinson and Fields 2004). In Florida, where it is a serious plant pest, *Z. provisoria* has also been reported as a host of *Angiostrongylus cantonensis* (Emerson et al. 2013; Stockdale-Walden et al. 2015; Stockdale Walden et al. 2017; Walden et al. 2021). Robinson and Fields (2004) noted that this species is often intercepted in horticultural shipments from Florida and warned that in Alabama, Mississippi, Louisiana, Texas, California, and Hawaii could easily become established and become a costly agricultural pest. Regrettably, their prediction of its potential establishment in the Hawaiian Islands may have now come to pass, particularly in view of its environmental compatibility.

On September 8, 2020, the HDOA contacted researchers in Malacology at BPBM requesting identification of snails found on the property of a private residence in Kaneohe, on the island of Oahu (Figure 2). Based on images from the HDOA, the snails were initially identified as *Zachrysia provisoria*. Researchers from BPBM accompanied HDOA staff to the residence on September 15, 2020, to conduct an extensive survey for the snails, recovering dozens of live specimens from all age classes, indicative of an established population. Subsequent discussion with the resident revealed that they first noticed the snails on the property “six to twelve months ago” following the purchase of a potted plant from a local garden store. A subsequent search of the garden store by HDOA staff recovered juveniles and adult snails.

On June 21, 2021, *Z. provisoria* was reported again by another private homeowner on the leeward side of the island who noticed the snail on a

recently purchased ti (*Cordyline fruticosa*) plant from a local nursery. Surveys by HDOA staff of the nursery where the potted plant was purchased turned up another half dozen live snails.

In December 2021 a third nursery, near the private residence in Kaneohe, where *Z. provisoria* was first recorded in 2020, reported a single live specimen on their property. A subsequent survey by BPBM researchers and HDOA staff failed to recover any additional specimens.

Multiple records of *Z. provisoria* and the recovery of various size classes at more than one site is indicative of an established breeding population. This species will probably continue to spread and be reported from additional locations in the future. Immediate eradication efforts are needed to prevent the spread on Oahu and to other islands.

Material examined:

USA – Hawaii, Honolulu County, Oahu • 7; Kaneohe; 9 Sep. 2020; Janis N. Matsunaga leg. BPBM 287520 • 13; Kaneohe; 11 Sep. 2020; Norine W. Yeung, Kenneth A. Hayes, Janis N. Matsunaga leg.; BPBM 287517 • 1; Kaneohe; 11 Sep. 2020; Norine W. Yeung, Kenneth A. Hayes, Janis N. Matsunaga leg.; USDA 131357 • 10; Kaneohe; 18 Sep. 2020; Janis N. Matsunaga leg.; BPBM 287523 • 1; Ewa Beach; 21 Jun. 2021; Sharla Tadeo, Ricarte Tadeo leg.; BPBM 288414 • 6; Hawaii Kai; 25 Jun. 2021; Janis N. Matsunaga leg.; BPBM 288417 • 1; Kaneohe; 3 Jan. 2022; Francis Joy leg.; BPBM 289079. – Florida, Broward County • 25; Fort Lauderdale; 2 Jun. 2018; John D. Slapcinsky leg.; BPBM 289149.

Discussion

DNA barcodes and phylogenetic analyses corroborate the morphological identifications of these two newly reported species introduced to Hawaii and provide some clues as to their potential origins. The *Otala lactea* from Hawaii are from two different source populations, one arriving via California on a vehicle shipped to Hawaii, and the other, potentially coming from established populations in Florida. All the sequences from US populations show close affinities for those from the Iberian Peninsula. *Zachrysia provisoria* appears to be most likely introduced from populations in Florida along with nursery trade materials, which is a well-known pathway for introduced species into Hawaii (Cowie et al. 2008).

Hawaii is one of the most isolated archipelagos in the world, a characteristic credited with helping drive the evolution of nearly 10,000 species of plants and animals unique to the islands (Eldredge and Evenhuis 2003). Successful, new colonization of the islands by plants and animals prior to human arrival has been estimated to be about once every 35,000–100,000 years (Fosberg 1948; Ziegler 2002). In contrast, in recent decades that rate has increased to an estimated at least one newly established species every 18

days, facilitated primarily through human transport (Ikuma et al. 2002). At least 22 plants are introduced per year, and more than 860 non-native plant species have become established in the last 300 years (Cordell 2021). By comparison, the more than 750 endemic species of land snails in Hawaii are thought to be the result of fewer than 23 colonization events over more than five million years, which is fewer than one successful dispersal event every 200,000 years (Zimmerman 1948; Ziegler 2002). Since 2008, 40 newly established non-marine, non-native snail species have been recorded in Hawaii (Kraus 2003; Hayes et al. 2007; Cowie et al. 2008; Hayes et al. 2012; Hayes et al. *unpublished data*). While some of these new records are the results of revised identifications to previously established taxa, others represent newly established species that probably existed in sleeper populations long before being detected. Sadly, none are welcome additions to the malacofauna, because in addition to the potential direct threats they pose to agriculture, commerce, and natural resources, they also bring with them a host of symbionts, many of which may be parasites or pathogens that cause zoonotic diseases, impacting wildlife and human health (Kim et al. 2014).

The intensified propagule pressure created by global commerce has increased the number of invasive species in Hawaii and throughout the world. The horticultural trade is a well-known pathway for newly introduced snails, and other pests (Cowie et al. 2008; Bergey et al. 2014). Well-established pathways, combined with insufficient funding for biosecurity and conservation programs, have created a situation where more introductions will go unreported prior to establishment, creating sleeper populations potentially leading to future economic and ecological damage more costly to mediate than the initial efforts aimed at early detection. The two examples reported here, large snails not easily overlooked for long, are only a small fraction of the species being introduced, with most going undetected, especially smaller, poorly studied species. The ability to rapidly identify and respond to the introduction and potential establishment of these two species of quarantine significance was possible, in part, because of the strong, but informal, collaborative relationship among BPBM researchers and state agencies charged with protecting natural resources in Hawaii. However, for such partnerships to be sustainable and effective, there needs to be long-term planning and support for them, including formal agreements, financial support via legislative action, and an appreciation of the importance of such relationships by the executive teams of all agencies involved. For example, at the Academy of Natural Sciences of Drexel University and the Smithsonian's National Museum of Natural History there are staff positions supported by the National Oceanic and Atmospheric Administration, USDA, and other agencies needing taxonomic expertise and reference collections to fulfill their missions. The establishment of formal positions and additional affiliate positions for jointly supported agency staff such as the HDOA, DLNR, and the USDA within BPBM would substantially benefit the efforts to secure and protect

our valuable natural resources. Leveraging the agency expertise and staffing along with the extensive collections and taxonomic expertise of the museum provides an economically feasible and a more tractable way to fulfill the mission of these agencies and the museum, and simultaneously contribute to building the capacity to address serious biosecurity issues facing the state.

Unfortunately, many agencies, much like most natural history museums, are understaffed and underfunded, leaving far too many of their collections misidentified, or worse unidentified, and in need of extensive curatorial care (Naggs 2022). Support for the basic foundation of all of biology, taxonomy, has been in decline for decades (Tahseen 2014; Ely et al. 2017), and there are no signs that this impediment will be addressed adequately in time to mitigate the ongoing and worsening biodiversity crisis (Cowie et al. 2022). The difficulties of identifying invasive species are further exacerbated by the fact that staff from state agencies often have taxonomic expertise in a few narrow groups and lack the resources to identify and understand the impacts of invasives broadly, particularly when they involve poorly studied groups like molluscs. As a result, introduced species continue to spread until they become serious pests, impacting agriculture, ecosystem services, or human health. Without early detection and mitigation or eradication, these pests are much more costly to control than they would be in the early establishment phase. Collaborative partnerships between natural history museums and natural resource management agencies at all levels can, in part, help alleviate some of these issues by sharing expertise and funding lines, while also helping fill the need for broad professional development of staff.

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Author’s contribution

All authors were involved in discussion of the manuscript conception. K.A.H., N.W.Y., and C.C.C. wrote the first draft and all authors contributed to editing and revising. K.A.H. completed the anatomical and phylogenetic analysis, and T.M.B.M. prepared images of live specimens and shells for figures. J.R.K. compiled historical records of introductions and verified specimens in the museum collection. All authors have read and agreed to the published version of the manuscript.

References

- Abreau CM (1998) New record of *Otala lactea* (Müller, 1774) Mollusca, Gastropoda in Madeira. *Bocagiana* 193: 1–3
- Aguayo CG (1944) *Leptinaria lamellata* y otros moluscos introducidos en Cuba. *Revista de la Sociedad Malacológica Carlos de la Torre* 2: 51–58
- Agudo-Padron I (2020) Moluscos exóticos no marinos “introducidos” en la isla caribeña de La Española (Hispaniola), Grandes Antillas: una aproximación a su conocimiento. *Revista Minerva* 3: 129–138, <https://doi.org/10.5377/revminerva.v3i1.12477>
- Alvarez S, Solís D (2018) Rapid response lowers eradication costs of invasive species. *Choices* 33(4): 1–9
- Araya JF (2015) Current status of the non-indigenous molluscs in Chile, with the first record of *Otala punctata* (Müller, 1774) (Gastropoda: Helicidae) in the country and new records for *Cornu aspersum* (Müller, 1774) and *Deroceras laeve* (Müller, 1774). *Journal of Natural History* 49: 1731–1761, <https://doi.org/10.1080/00222933.2015.1006703>
- Auffenberg K, Stange LA (1993) The Camaenidae (Mollusca: Pulmonata) of Florida. Florida Department of Agriculture and Consumer Services. Entomology Circular 356, 2 pp
- Auffenberg K, Stange LA, Capinera JL, White J (2011) Pleurodontid snails of Florida, *Caracolus marginella* (Gmelin), *Zachrysia provisoria* (L. Pfeiffer), *Zachrysia trinitaria* (L. Pfeiffer), (Gastropoda: Pleurodontidae). Entomology and Nematology Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, EENY-118, 3 pp
- Backhuys W (1975) Zoogeography and taxonomy of the land and freshwater molluscs of the Azores. Backhuys and Meesters, Amsterdam, 350 pp, 97 maps, 32 pls
- Barbara N, Schembri PJ (2008) The status of *Otala punctata* (Müller, 1774), a recently established terrestrial gastropod in Malta. *Bollettino Malacologico* 44: 101–107
- Beckmann K-H (2007) Die Land- und Süßwassermollusken der Balearischen Inseln. Conchbooks, Hackenheim, Germany, 255 pp
- Bendall W (1895) A list of the land Mollusca of the island of New Providence, Bahamas, with an enumeration of the species recorded from the other islands. *Proceedings of the Malacological Society of London* 1: 292–295
- Bequaert J, Miller WB (1973) The mollusks of the arid Southwest, with an Arizona check list. University of Arizona Press, Tucson, USA, xvi + 271 pp
- Bergey EA, Figueroa LL, Mather CM, Martin RJ, Ray EJ, Kurien JT, Westrop DR, Suriyawong P (2014) Trading in snails: plant nurseries as transport hubs for non-native species. *Biological Invasions* 16: 1441–1451, <https://doi.org/10.1007/s10530-013-0581-1>
- Berrag B, Urquhart GM (1996) Epidemiological aspects of lungworm infections of goats in Morocco. *Veterinary Parasitology* 61: 81–95, [https://doi.org/10.1016/0304-4017\(95\)00803-9](https://doi.org/10.1016/0304-4017(95)00803-9)
- Bertrand A (2001) Notes sur les mollusques terrestres de Saint-Martin (Petites Antilles). *Documents Malacologiques* 2: 35–37
- Bieler R, Slapcinsky J (2000) A case study for the development of an island fauna: recent terrestrial mollusks of Bermuda. *Nemouria, Occasional Papers of the Delaware Museum of Natural History* 44: 1–100
- Binney WG (1885) A manual of American land shells. Bulletin of the United States National Museum 28. US Government Printing Office, 528 pp, <https://doi.org/10.5479/si.03629236.28.1>
- Blacket MJ, Shea M, Semeraro L, Malipatil MB (2016) Introduced Helicidae garden snails in Australia: morphological and molecular diagnostics, species distributions and systematics. *Records of the Australian Museum* 68: 99–116, <https://doi.org/10.3853/j.2201-4349.68.2016.1648>
- Bland T (1862) On the geographical distribution of the genera and species of land shells of the West India Islands; with a catalogue of the species of each island. *Annals of the Lyceum of Natural History of New York* 7: 335–361, <https://doi.org/10.1111/j.1749-6632.1862.tb00164.x>
- Breure ASH, Hovestadt A, Fields A, Robinson DG (2016) The land Mollusca (Gastropoda) of Saint Kitts and Nevis (Lesser Antilles), with description of a new species. *The Nautilus* 130: 27–52
- Burch JB (1976) Outline of classification of Australian terrestrial molluscs (native and introduced). *Journal of the Malacological Society of Australia* 3: 127–156, <https://doi.org/10.1080/00852988.1976.10673889>
- Büyüktaktakın İE, Haight RG (2018) A review of operations research models in invasive species management: state of the art, challenges, and future directions. *Annals of Operations Research* 271: 357–403, <https://doi.org/10.1007/s10479-017-2670-5>
- Cabaret J (1979) Réceptivité expérimentale à l'infestation par les larves de Protostrongylidés de quelques Hélicides fréquents au Maroc. *Annales de Parasitologie (Paris)* 54: 475–482, <https://doi.org/10.1051/parasite/1979544475>
- Cabaret J (1988) Natural infection of landsnails on pasture grazed by sheep in the Rabat area (Morocco). *Veterinary Parasitology* 26: 297–304, [https://doi.org/10.1016/0304-4017\(88\)90098-2](https://doi.org/10.1016/0304-4017(88)90098-2)
- Cabaret J, Dakkak A, Bahaida B (1980) Etude de l'infestation des mollusques terrestres de la région de Rabat (Maroc) par les larves de protostrongylidés dans les conditions naturelles. *Revue d'Élevage et de Médecine Vétérinaire des Pays Tropicaux* 33: 159–165

- Cadevall J, Orozco A (2016) Caracoles y babosas de la Península Ibérica y Baleares. Nuevas Guías de Campo Omega, Barcelona, Spain, 817 pp
- Cameron RAD, Pokryszko BM, Frias Martins AM (2012) Land snail faunas on Santa Maria (Azores): local diversity in an old, isolated and disturbed island. *Journal of Molluscan Studies* 78: 268–274, <https://doi.org/10.1093/mollus/ey009>
- Campos J, Calvo A (2006) Molluscos introducidos en Uruguay. *Comunicaciones de la Sociedad Malacologica del Uruguay* 9: 75–78
- Capinera JL (2013) Cuban brown snail, *Zachrysia provisoria* (Gastropoda): damage potential and control. *Crop Protection* 52: 57–63, <https://doi.org/10.1016/j.cropro.2013.05.014>
- Capinera JL, White J (2011) Terrestrial snails affecting plants in Florida. Department of Entomology, University of Florida. EENY- 497, 12 pp, <https://doi.org/10.32473/edis-in893-2011>
- Charles L (2016) Inventaire des mollusques terrestres de Guadeloupe, Petites Antilles: données préliminaires. *MalaCo* 12: 47–56
- Chase R, Robinson DG (2001) The uncertain history of land snails on Barbados: implications for conservation. *Malacologia* 43: 33–57
- Chellat S, Toubal L, Djerrab A, Bourefis A, Hamdi-Aissa B, Salmi-laouar S (2018) Molluscan and sedimentological sequences of the late Quaternary deposits of Morsott region (NE Algeria) and their paleoenvironmental implication. *BSGF-Earth Sciences Bulletin* 189: 17, <https://doi.org/10.1051/bsgf/2018016>
- Cilia DP (2012) Contributions to the malacology of Malta, II: on the second record of *Otala punctata* (Müller, 1774) (Gastropoda: Helicidae) from Malta. *The Central Mediterranean Naturalist* 5: 4–5
- Civeyrel L, Simberloff D (1996) A tale of two snails: is the cure worse than the disease? *Biodiversity and Conservation* 5: 1231–1252, <https://doi.org/10.1007/BF00051574>
- Clapp GH (1919) Cuban mollusks colonized in Florida. *The Nautilus* 32(3): 104–105
- Clarke R (1957) *Zachrysia provisoria* (Pfr.). *The Nautilus* 70: 142–143
- Clench WJ (1938) Land and freshwater mollusks of Grand Bahama and Abaco Islands, Bahama Islands. *Memorias de la Sociedad Cubana de Historia Natural “Felipe Poey”* 12: 303–333, pls 24–25
- Clench WJ (1959) *Zachrysia auricoma* (Férussac) in Miami, Florida. *The Nautilus* 73: 76
- Clench WJ (1960) *Zachrysia provisoria* (Pfr.) in Homestead, Florida. *The Nautilus* 73(4): 3
- Connolly M (1939) A monographic survey of South African non-marine Mollusca. *Annals of the South African Museum* 33: 1–660
- Cordell S (2021) Regional Summaries: Hawaii and US-Affiliated Pacific Islands. In: Poland TM, Patel-Weyand T, Finch DM, Ford Miniati C, Hayes DC, Lopez VM (eds), *Invasive Species in Forests and Rangelands of the United States: A Comprehensive Science Synthesis for the United States Forest Sector*. Springer International Publishing, Heidelberg, Germany, pp 343–351
- Cortéz-Sánchez M, Morales-Muñoz A, Simón-Vallejo MD, Mercè Bergadà-Zapata M, Delgado-Huertas A, López-García P, López-Sáez JA, Carmen Lozano-Francisco M, Riquelme-Cantal JA, Roselló-Izquierdo E, Sánchez-Marco A, Vera-Peláez JL (2008) Palaeoenvironmental and cultural dynamics of the coast of Málaga (Andalusia, Spain) during the Upper Pleistocene and early Holocene. *Quaternary Science Reviews* 27: 2176–2193, <https://doi.org/10.1016/j.quascirev.2008.03.010>
- Cortéz-Sánchez M, Simón-Vallejo MD, Jiménez-Espejo FJ, Lozano Francisco MC, Vera-Peláez JL, Maestro González A, Morales-Muñoz A (2019) Shellfish collection on the westernmost Mediterranean, Bajondillo cave (~160–35 cal kyr BP): a case of behavioral convergence? *Quaternary Science Reviews* 217: 284–296, <https://doi.org/10.1016/j.quascirev.2019.02.007>
- Cortéz-Sánchez M, Calle Román L, Simón-Vallejo MD, Lozano-Francisco MC, Riquelme Cantal JA, Vera-Peláez JL, Parilla Giráldez R, Macías Tejada S (2020) On the shore of Mediterranean Sea. The end of the palaeolithic on the coast of Málaga (South of Spain). *Quaternary International* 564: 94–99, <https://doi.org/10.1016/j.quaint.2019.11.028>
- Cowie RH, Hayes KA, Tran CT, Meyer WM III (2008) The horticultural industry as a vector of alien snails and slugs: widespread invasions in Hawaii. *International Journal of Pest Management* 54: 267–276, <https://doi.org/10.1080/09670870802403986>
- Cowie RH, Dillon RT, Robinson DG, Smith JW (2009) Alien non-marine snails and slugs of priority quarantine importance in the United States: a preliminary risk assessment. *American Malacological Bulletin* 27: 113–132, <https://doi.org/10.4003/006.027.0210>
- Cowie RH, Bouchet P, Fontaine B (2022) The Sixth Mass Extinction: fact, fiction or speculation? *Biological Reviews* 97: 640–663, <https://doi.org/10.1111/brv.12816>
- d'Orbigny A (1835) Synopsis terrestrium, et fluviatilium molluscorum, in suo per Americam meridionalem itinerere, ab A. d'Orbigny collectorum. *Magasin de Zoologie* 5(61/62): 1–44
- Deisler JE, Abbott RT (1984) Range extensions of some introduced land mollusks in the Bahama Islands, with first reports for four species. *The Nautilus* 98: 12–17
- Diagne C, Catford JA, Essl F, Nuñez MA, Courchamp F (2020) What are the economic costs of biological invasions? A complex topic requiring international and interdisciplinary expertise. *NeoBiota* 63: 25–37, <https://doi.org/10.3897/neobiota.63.55260>

- Doleman PS (1973) Collections made in association with C.S.S. Dawson Cruise 72-004. Nova Scotia Museum Curatorial Report 12, 14 pp, 4 figs, 3 maps
- Dundee DS, Watt P (1961) Louisiana land snails with new records. *The Nautilus* 75: 79–83
- Durkan TH, Yeung NW, Meyer WM III, Hayes KA, Cowie RH (2013) Evaluating the efficacy of land snail survey techniques in Hawaii: implications for conservation throughout the Pacific. *Biodiversity and Conservation* 22: 3223–3232, <https://doi.org/10.1007/s10531-013-0580-7>
- Eldredge LG, Evenhuis NL (2003) Hawaii's biodiversity: a detailed assessment of the numbers of species in the Hawaiian Islands. *Bishop Museum Occasional Papers* 76: 1–30
- Ely CV, de Loreto Bordignon SA, Trevisan R, Boldrini II (2017) Implications of poor taxonomy in conservation. *Journal for Nature Conservation* 36: 10–13, <https://doi.org/10.1016/j.jnc.2017.01.003>
- Emerson JA, Stockdale Walden H, Peters RK, Farina LL, Fredholm DV, Qvarnstrom Y, Xayavong M, Bishop H, Slapcinsky J, McIntosh A, Wellehan JFX Jr (2013) Eosinophilic meningoencephalomyelitis in an orangutan (*Pongo pygmaeus*) caused by *Angiostrongylus cantonensis*. *Veterinary Quarterly* 33: 191–194, <https://doi.org/10.1080/01652176.2013.880005>
- Espinosa A, Robinson DG (2021) Annotated checklist of the terrestrial mollusks (Mollusca: Gastropoda) from Hispaniola Island. *Novitates Caribaea* 17: 71–146, <https://doi.org/10.33800/nc.vi17.250>
- Espinosa J, Ortea J (1999) Moluscos terrestres del archipiélago Cubano. *Avicennia* Suppl 2: 1–137
- Felix ZI, Dubuc MA, Rana HA (2019) A tentative list of the land snails of Georgia, U.S.A. *Georgia Journal of Science* 77(2): 8
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3(5): 294–299
- Fosberg FR (1948) Immigrant plants in the Hawaiian Islands. II. *University of Hawaii Occasional Papers* 46: 3–17, <https://doi.org/10.5962/bhl.title.112334>
- Fukuda H, Haga TA, Tatara YU (2008) Niku-nuku: a useful method for anatomical and DNA studies on shell-bearing molluscs *Zoosymposia* 1: 15–38, <https://doi.org/10.11646/zoosymposia.1.1.5>
- Gammon ET (1943) Helicid snails in California. *The Bulletin, California Department of Agriculture* 32: 173–187
- García-Rivero D, Pérez-Jordà G, García-Viñas E, López-Sáez JA, Taylor R, Peña-Chocarro L, Bernáldez-Sánchez E, Pérez-Díaz S (2019) Ecological patterns and use of natural resources during the Neolithic of the south of the Iberian Peninsula: an update from the 6th to 4th millennia cal BC sequence of Dehesilla Cave. *Quaternary Science Reviews* 219: 218–235, <https://doi.org/10.1016/j.quascirev.2019.07.010>
- Gould SJ (1969) An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bulletin of the Museum of Comparative Zoology* 138: 407–531, frontis, pls. 1-5
- Grimm FW (1964) *Otala lactea* in Virginia, Texas, and California. *The Nautilus* 77: 108, iii
- Groh K (1983) Revision der Land- und Süßwassergastropoden der Kapverdischen Inseln. *Archiv für Molluskenkunde* 113: 159–223
- Groh K (1985) Landschnecken aus quartären Wirbeltierfundstellen der Kanarischen Inseln (Gastropoda). *Bonner zoologische Beiträge* 36: 395–415
- Hanna GD (1966) Introduced mollusks of western North America. *Occasional Papers of the California Academy of Sciences* 48: 1–48
- Harry HW (1948) Notes on the foreign land snails of Louisiana. *The Nautilus* 62: 20–24
- Hayes KA, Tran CT, Cowie RH (2007) New records of alien Mollusca in the Hawaiian Islands: nonmarine snails and slugs (Gastropoda) associated with the horticultural trade. *Bishop Museum Occasional Papers* 96: 54–63
- Hayes KA, Yeung NW, Kim JR, Cowie RH (2012) New records of alien Gastropoda in the Hawaiian Islands: 1996–2010. *Bishop Museum Occasional Papers* 112: 21–28
- Henderson J (1936) *Helix axia* Bgt. and *Helix lactea* Müller in Florida. *The Nautilus* 50: 72
- Herbert DG (2010) The introduced terrestrial Mollusca of South Africa. South African National Biodiversity Institute, Pretoria. SANBI Biodiversity Series 15, vi + 108 pp
- Herbert DG, Sirgel WF (2001) The recent introduction of two potentially pestiferous alien snails into South Africa and the outcomes of different pest management practices: an eradication and a colonization. *South African Journal of Science* 97: 301–304
- Hill HR (1941) New records of introduced land shells in Southern California. *The Nautilus* 55: 31
- Holyoak DT, Holyoak GA (2017) A revision of the land snail genera *Otala* and *Eobania* (Gastropoda: Helicidae) in Morocco and Algeria. *Journal of Conchology* 42: 419–490
- Holyoak DT, Holyoak GA, Mendes RM da C (2019) A revised check-list of the land and freshwater Mollusca (Gastropoda and Bivalvia) of mainland Portugal. *Iberus* 37: 113–168
- Hovestadt A, Neckheim CM (2020) A critical checklist of the non-marine molluscs of St. Martin, with notes on the terrestrial malacofauna of Anguilla and Saint-Barthélemy, and the description of a new subspecies. *Folia Conchylologica* 57: 1–38
- Hovestadt A, van Leeuwen S (2017) Terrestrial molluscs of Aruba, Bonaire and Curaçao in the Dutch Caribbean: an updated checklist and guide to identification. *Vita Malacologica* 16: 1–39
- Hubricht L (1963) *Otala lactea* at Vicksburg, Miss. *The Nautilus* 76: 110

- Hutterer R, Linstädter J, Eiwanger J, Mikdad A (2014) Human manipulation of terrestrial gastropods in Neolithic culture groups of NE Morocco. *Quaternary International* 320: 83–91, <https://doi.org/10.1016/j.quaint.2013.12.006>
- Ikuma EK, Sugano D, Mardfin JK (2002) Filling the gaps in the fight against invasive species. Honolulu, HI: Legislative Reference Bureau 122 pp, <https://lrh.hawaii.gov>
- Jackson RW (1944) *Otala vermiculata* Muller and *O. lactea* Muller in Texas. *The Nautilus* 57: 105
- Jacobson MK (1965) On some land shells of Eleuthera, Bahamas. *The Nautilus* 78: 120–125
- Jaume AF, Bernad DR, Xamena DV (2011) Fauna, flora i minerals de les Balears a l'anglès: fonts literàries, fonts científiques i fonts arqueològiques. I. La grua Balear i els caragols. *Bolletí de la Societat Arqueològica Lulliana* 67: 39–53 [In Catalan with English abstract]
- Jindrak K, Mansukhani MG, Freiberg A (1977) Commercially available, edible snails *Otala lactea* (Müller) and *Helix aperta* (Born) as laboratory hosts of *Angiostrongylus cantonensis*. *Journal of Parasitology* 63: 1132–1133, <https://doi.org/10.2307/3279869>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780, <https://doi.org/10.1093/molbev/mst010>
- Kim JR, Hayes KA, Yeung NW, Cowie RH (2014) Diverse gastropod hosts of *Angiostrongylus cantonensis*, the rat lungworm, globally and with a focus on the Hawaiian Islands. *PLoS ONE* 9: e94969, <https://doi.org/10.1371/journal.pone.0094969>
- Kraus F (2003) New records of alien plants and animals in Hawaii. *Bishop Museum Occasional Papers* 74: 76–78
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549, <https://doi.org/10.1093/molbev/msy096>
- Larson ER, Graham BM, Achury R, Coon JJ, Daniels MK, Gambrell DK, Jonasen KL, King GD, LaRacunte N, Perrin-Stowe TI, Reed EM (2020) From eDNA to citizen science: emerging tools for the early detection of invasive species. *Frontiers in Ecology and the Environment* 18: 194–202, <https://doi.org/10.1002/fee.2162>
- Limondin-Lozouet N, Haddoumi H, Lefèvre D, Ghamizi M, Aouraghe H, Salel T (2013) Holocene molluscan succession from NE Morocco: palaeoenvironmental reconstruction and biogeographical implications. *Quaternary International* 302: 61–76, <https://doi.org/10.1016/j.quaint.2012.11.036>
- Lyal CHC, Miller SE (2019) Capacity of United States federal government and its partners to rapidly and accurately report the identity (taxonomy) of non-native organisms intercepted in early detection programs. *Biological Invasions* 22: 101–127, <https://doi.org/10.1007/s10530-019-02147-x>
- Maciera D, Miquel SE, Espinosa J, Virgillito M, Lauranzón B (2013) Moluscos terrestres y primera cita de la familia Punctidae (Mollusca: Pulmonata: Gastropoda) y de sue especie *Paralaoma servilis* para Cuba. *Solenodon* 11: 95–102
- Marsico TD, Burt JW, Espeland EK, Gilchrist GW, Jamieson MA, Lindström L, Roderick GK, Swope S, Szűcs M, Tsutsui ND (2010) PERSPECTIVE: Underutilized resources for studying the evolution of invasive species during their introduction, establishment, and lag phases. *Evolutionary Applications* 3: 203–219, <https://doi.org/10.1111/j.1752-4571.2009.00101.x>
- Massemin D, Pointier J-P (2010) Ces escargots qui envahissent la Guadeloupe. *Le Courrier de la Nature* 254: 16–17
- Mead AR (1971) Helicid land mollusks introduced into North America. *The Biologist* 53: 104–111
- Melville JC, Ponsonby JH (1898) A contribution towards a check-list of the non-marine molluscan fauna of South Africa. *Proceedings of the Malacological Society of London* 3: 166–184, <https://doi.org/10.1093/oxfordjournals.mollus.a065163>
- Mercadel B, Villalta JF, Obrador A, Rosell J (1970) Nueva aportación al conocimiento del Cuaternario menorquín. *Acta Geologica Hispanica* 5: 89–93
- Mienis HK (2001) Wie bezit informatie betreffende landslakken uit het geslacht *Otala* van Amerikaanse vindplaatsen? *Spirula* 320: 57 [in Dutch with English abstract]
- Mifsud C, Sammut P, Cachia C (2003) On some alien terrestrial and freshwater gastropods (Mollusca) from Malta. *The Central Mediterranean Naturalist* 4: 35–40
- Murray HD (1968) *Otala lactea* in San Antonio, Texas. *The Nautilus* 81: 141–143
- Naggs F (2022) The tragedy of the Natural History Museum, London. *Megataxa* 7: 86–112, <https://doi.org/10.11646/megataxa.7.1.2>
- Naranjo-García E, Castillo-Rodríguez ZG (2017) First inventory of the introduced and invasive mollusks in Mexico. *The Nautilus* 131: 107–126
- Neckheim CM, Hovestadt A (2016) Land-en zoetwatermollusken verzameld op Sint Maarten (Nederlandse Antillen) en Saint Martin. *Spirula* 409: 18–24
- Paul CRC (1984) Pleistocene non-Marine molluscs from Cova de Ca Na Reia, Eivissa. *Bolletí de la Societat d'Historia Natural de les Balears* 28: 95–114
- Pérez AM, Espinoza J (1993) Catálogo, claves y bibliografía de la familia Camaenidae (Pulmonata: Stylommatophora) en Cuba. *Revista de Biología Tropical* 41: 667–681

- Pilsbry HA (1889) Manual of Conchology. Structural and systematic. With illustrations of the species. Founded by George W. Tryon, Jr. Second series: Pulmonata. Vol. V. Helicidae: Vol. III. Academy of Natural Sciences of Philadelphia, Philadelphia, USA, 216 pp, 64 pls
- Pilsbry HA (1928) Studies on West Indian mollusks: the genus *Zachrysis*. *Proceedings of the Philadelphia Academy of Natural Sciences* 80: 581–606
- Pilsbry HA (1939) Land Mollusca of North America (north of Mexico). Vol. 1, Pt. 1. Academy of Natural Sciences of Philadelphia, Monographs 3. pp i–xvii, 1–573, i–iv
- Pinkerton MG, Thompson SM, Casuso NA, Hodges AC, Leppla NC (2019) Engaging Florida's youth to increase their knowledge of invasive species and plant biosecurity. *Journal of Integrated Pest Management* 10: 1–7, <https://doi.org/10.1093/jipm/pmy019>
- Pratt WL, Jr. (1964) Some Texas localities for Helicidae. *The Nautilus* 78: 32–33
- Quintana J (2001) Fauna malacológica presente en los sedimentos holocénicos de Barranc d'Algender (Ferrerries, Menorca). *Spira* 1: 33–40
- Quintana J (2006) Molluscs terrestres autòctons i introduïts a l'illa de Menorca (Illes Balears, Mediterrània occidental). *Spira* 2: 17–26
- Rabaglia RJ, Cognato AI, Hoebeke ER, Johnson CW, LaBonte JR, Carter ME, Vlach JJ (2019) Early detection and rapid response: a 10-year summary of the USDA Forest Service program of surveillance for non-native bark and ambrosia beetles. *American Entomologist* 65: 29–42, <https://doi.org/10.1093/ae/tmz015>
- Ramos J, Domínguez-Bella S, Cantillo JJ, Soriguer M, Pérez M, Hernando J, Vijande E, Zabala C, Clemente I, Bernal D (2011) Marine resources exploitation by Paleolithic hunter-fisher-gatherers and Neolithic tribal societies in the historical region of the Strait of Gibraltar. *Quaternary International* 239: 104–113, <https://doi.org/10.1016/j.quaint.2011.03.015>
- Reaser JK, Burgiel SW, Kirkey J, Brantley KA, Veatch SD, Burgos-Rodríguez J (2020) The early detection of and rapid response (EDRR) to invasive species: a conceptual framework and federal capacities assessment. *Biological Invasions* 22: 1–19, <https://doi.org/10.1007/s10530-019-02156-w>
- Republica Dominicana, Ministerio de Medio Ambiente (2012) Estrategia Nacional de Especies Exóticas Invasoras Realizado en el marco del Proyecto "Mitigando las amenazas de las especies exóticas invasoras en el Caribe Insular". Santo Domingo, República Dominicana, 35 pp
- Rosenberg G, Muratov IV (2006) [dated 2005] Status report on the terrestrial Mollusca of Jamaica. *Proceedings of the Academy of Natural Sciences of Philadelphia* 155: 117–161, <https://doi.org/10.1635/i0097-3157-155-1-117.1>
- Rosselló VM, Cuerda J (1973) Notas sobre el Plioceno y Cuaternario del Banc d'Eivissa (Mallorca). *Cuadernos de Geografía de la Universitat de Valencia* 13: 5–13, pls 1–3
- Roth B, Sadeghian PS (2006) Checklist of the land snails and slugs of California, second ed. Santa Barbara Museum of Natural History Contributions in Science 3, 81 pp
- Rumi A, Sánchez J, Ferrando NS (2010) *Theba pisana* (Müller, 1774) (Gastropoda, Helicidae) and other alien land molluscs species in Argentina. *Biological Invasions* 12: 2985–2990, <https://doi.org/10.1007/s10530-010-9715-x>
- Rush WH (1892) Extracts from a letter to the editor from Dr. Wm. H. Rush. *The Nautilus* 6: 81–82
- Saafi I, Aouadi N, Dupont C, Belhouchet L (2013) L'économie de subsistance dans la cuvette de Meknassy (Sidi Bouzid, Tunisie centrale) durant l'Holocène d'après l'étude malacologique. *Bulletin de la Société préhistorique française* 110: 703–718, <https://doi.org/10.3406/bspf.2013.14321>
- Say T (1822) Description of univalve terrestrial and fluviatile shells of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 2: 370–381
- Schileyko AA (2006) Treatise on recent terrestrial pulmonate molluscs. Part 13. Helicidae, Pleurodontidae, Polygyridae, Ammonitellidae, Oreohelicidae, Thysanophoridae. *Ruthenica Supplement* 2 13: 1765–1906
- Schindel DE, Cook JA (2018) The next generation of natural history collections. *PLoS Biology* 16: e2006125, <https://doi.org/10.1371/journal.pbio.2006125>
- Seddon MB (2008) The landsnails of Madeira. An illustrated compendium of the landsnails and of the Madeiran archipelago. Studies in Biodiversity and Systematics of Terrestrial Organisms from the National Museum of Wales. *Biotir Reports* 2: 1–204
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 1–9, <https://doi.org/10.1038/ncomms14435>
- Serrano F, Guerra-Merchán A, Lozano-Francisco C, Vera-Peláez JL (1997) Multivariate analysis of remains of molluscan foods consumed by Latest Pleistocene and Holocene humans in Nerja Cave, Málaga, Spain. *Quaternary Research* 48: 215–227, <https://doi.org/10.1006/qres.1997.1920>
- Shultz AJ, Adams BJ, Bell KC, Ludt WB, Pauly GB, Vendetti JE (2021) Natural history collections are critical resources for contemporary and future studies of urban evolution. *Evolutionary Applications* 14: 233–247, <https://doi.org/10.1111/eva.13045>
- Simmonds FJ, Hughes IW (1963) Biological control of snails exerted by *Euglandina rosea* (Ferussac) in Bermuda. *Entomophaga* 8: 219–222, <https://doi.org/10.1007/BF02376092>
- Smith BJ (1992) Zoological catalogue of Australia, vol. 8: non-marine Mollusca. Australian Government Printing Service, Canberra, Australia, 285 pp

- Spear MJ, Walsh JR, Ricciardi A, Zanden MJV (2021) The invasion ecology of sleeper populations: Prevalence, persistence, and abrupt shifts. *BioScience* 71: 357–369, <https://doi.org/10.1093/biosci/biaa168>
- Stockdale Walden HD, Slapcinsky JD, Roff S, Mendieta Calle J, Diaz Goodwin Z, Stern J, Corlett R, Conway J, McIntosh A (2017) Geographic distribution of *Angiostrongylus cantonensis* in wild rats (*Rattus rattus*) and terrestrial snails in Florida, USA. *PLoS ONE* 12: e0177910, <https://doi.org/10.1371/journal.pone.0177910>
- Stockdale-Walden HD, Slapcinsky J, Qvarnstrom Y, McIntosh A, Bishop HS, Rosseland B (2015) *Angiostrongylus cantonensis* in introduced gastropods in southern Florida. *Journal of Parasitology* 101: 156–159, <https://doi.org/10.1645/14-553.1>
- Strecker JK Jr (1935) Land and fresh-water snails of Texas. *Transactions of Texas Academy of Science* 17: 5–44, pls 1–3
- Tahseen Q (2014) Taxonomy—the crucial yet misunderstood and disregarded tool for studying biodiversity. *Journal of Biodiversity and Endangered Species* 2: 128, <https://doi.org/10.4172/2332-2543.1000128>
- Tryon GW Jr (1888) Manual of Conchology. Structural and systematic. With illustrations of the species. Second series: Pulmonata. Vol. IV. Helicidae: Vol. II. Academy of Natural Sciences of Philadelphia, Philadelphia, USA, 296 pp, 69 pls
- USDA-APHIS (1999) United States Department of Agriculture, Animal and Plant Health Inspection Service. Importation and interstate movement of live, edible land snails: *Cantareus apertus* (Born), *Cryptomphalus aspersus* (Müller), *Eobania vermiculata* (Müller), *Helix pomatia* Linné, and *Otala lactea* (Müller) (Pulmonata: Helicidae). Qualitative pest risk analysis. Unpaginated [45 pp]
- van Buurt GV (2016) Field observations on some Curaçao landsnails, and new records for its fauna. *Folia Conchylologica* 34: 1–16
- van der Schalie H (1938) On the occurrence of *Helix lactea* Muller in North America. *The Nautilus* 51: 132–134
- van Leeuwen S, Boekken M, Hovestadt A (2015) De landslakken van Saba. *Spirula* 404: 23–30
- Vendetti JE, Lee C, LaFollette P (2018) Five new records of introduced terrestrial gastropods in southern California discovered by citizen science. *American Malacological Bulletin* 36: 232–247, <https://doi.org/10.4003/006.036.0204>
- Vendetti JE, Burnett E, Carlton L, Curran AT, Lee C, Matsumoto R, Mc Donnell R, Reich I, Willadsen O (2019) The introduced terrestrial slugs *Ambigolimax nyctelius* (Bourguignat, 1861) and *Ambigolimax valentianus* (Férussac, 1821) (Gastropoda: Limacidae) in California, with a discussion of taxonomy, systematics, and discovery by citizen science. *Journal of Natural History* 53: 1607–1632, <https://doi.org/10.1080/00222933.2018.1536230>
- Vicens D, Pons GX (2011) Els invertebrats terrestres fòssils als jaciments d'origen càrstic de illes Balears. *Endins* 35: 283–298
- Vicens D, Pons GX (2017) Registro fòsil del Cuaternario litoral de Menorca. In: Gómez-Pujol L, Pons GX (eds), Geomorfologia litoral de Menorca: dinàmica y practices de gestian. Societat d'Història Natural de Balears, Palma, Spain. *Monografia de la Societat d'Història Natural de les Balears* 25: 157–190
- Walden HDS, Slapcinsky J, Rosenberg J, Wellehan JF (2021) *Angiostrongylus cantonensis* (rat lungworm) in Florida, USA: Current status. *Parasitology* 148: 149–152, <https://doi.org/10.1017/S0031182020001286>
- Walsh JR, Munoz SE, Vander Zanden MJ (2016) Outbreak of an undetected invasive species triggered by a climate anomaly. *Ecosphere* 7: e01628, <https://doi.org/10.1002/ecs2.1628>
- Wang S, Loreau M, de Mazancourt C, Isbell F, Beierkuhnlein C, Connolly J, Deutschman DH, Doležal J, Eisenhauer N, Hector A, Jentsch A (2021) Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. *Ecology* 102: e03332, <https://doi.org/10.1002/ecy.3332>
- Ziegler AC (2002) Hawaiian natural history, ecology, and evolution. University of Hawaii Press, Honolulu, USA, 512 pp
- Zimmerman EC (1948) Insects of Hawaii, Vol. 1. Introduction. University of Hawaii Press, Honolulu, USA, 206 pp

Web sites and online databases

- Bank RA, Neubert E (2017) MolluscaBase—checklist of the land and freshwater Gastropoda of Europe. <https://www.molluscabase.org/aphia.php?p=sourceget&andid=279050> (accessed 28 February 2021)
- Robinson DG, Fields HA (2004) The Cuban garden snail *Zachrysis*: the emerging awareness of a [sic] important snail pest in the Caribbean Basin. https://www.researchgate.net/publication/268817356_The_Cuban_land_snail_Zachrysis_The_emerging_awareness_of_an_important_snail_pest_in_the_Caribbean_Basin (accessed 11 March 2021)
- Pandey RK, Dhar A (2013) Snail infestation of mulberry (*Morus alba*) in high water table area of Kathua (Jammu and Kashmir) during monsoon season. The Silkworm. <http://silkwormmori.blogspot.com/2013/10/snail-infestation-on-mulberry-morus.html> (accessed 14 March 2021)