

Rapid Communication**The wandering snaggletooth snail, *Gastrocopta servilis* (Gould, 1843) – a new record of an alien non-marine mollusc in South Africa (Gastropoda: Eupulmonata: Gastrocoptidae)**David G. Herbert^{1,2,*} and Sandi Willows-Munro²¹Department of Natural Sciences, National Museum Wales, Cathays Park, Cardiff, CF10 3NP, UK²School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, 3206, South Africa

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OPEN ACCESS**Abstract**

The widespread tropical tramp snail *Gastrocopta servilis* is recorded for the first time in South Africa. This represents the first record of the species from the continent of Africa. Specimens found in abundance in a remnant of natural habitat in Durban in 2011 could not be identified with any indigenous or introduced species known from eastern South Africa, suggesting that the species involved may represent an unrecorded introduction. Subsequent morphological study led to the material being identified as *G. servilis*. This identification was confirmed by comparison of sequence data from the mitochondrial DNA cytochrome *c* oxidase subunit I gene obtained for this material with that of other *Gastrocopta* species. Although this is the first record of the species from the seaboard of the western Indian Ocean, it is likely that other *Gastrocopta* species described from islands in this region are in reality pseudoindigenous taxa representing further introduced populations of the globally widespread *G. servilis*.

Key words: land snail, non-native, introduction, Africa, eastern seaboard**Introduction**

The discovery of an unfamiliar species of gastrocoptid snail in remnant natural habitat in an urban park in Durban (eThekweni Metro) has prompted further investigation. The species appeared referable to the genus *Gastrocopta* Wollaston, 1878, but it could not be matched with any of the currently known indigenous *Gastrocopta* species recorded from southern Africa (Connolly 1939). The snails were present in considerable abundance and their discovery in a disturbed urban location, close to one of the busiest ports in Africa, suggested a strong possibility that the material belonged to a population of a newly introduced species, or at least one that had not to date been discovered. The Durban area is well known from a malacological perspective and the possibility of an undescribed, but common indigenous species having remained undiscovered up to this point seemed remote. Morphological comparison of this material with other *Gastrocopta* species led to its identification as the tramp species

Gastrocopta servilis (Gould, 1843) and subsequent analyses of molecular data has confirmed this. Additional unidentified *Gastrocopta* specimens in the KwaZulu-Natal Museum Mollusca collection have since proven to belong to the same species.

The aim of this paper is to document the occurrence of *Gastrocopta servilis* as an introduced species in South Africa. This is the first record of this widespread tramp species from the African continent. We also draw attention to the fact that the species may well have been present on many of the islands in the south-western Indian Ocean for as long as 150 years, hiding in the guise of pseudoindigenous taxa (Carlton 2009) – something that remains to be investigated using molecular techniques.

Materials and methods

All material examined is housed in the KwaZulu-Natal Museum, Pietermaritzburg (NMSA). For SEM examination, shells were mounted on stubs, coated with gold-palladium, and examined at low accelerating voltage (5 kV) in a Zeiss EVO 10LS scanning electron microscope. Specimens were initially identified on the basis of shell colour and morphology, in particular whorl curvature, and the extent of sutural indentation, the number, position, shape and size of apertural barriers, and details of external whorl sculpture. For molecular confirmation of the identification, a subsample of snails was preserved in 99% ethanol and then sent to the Canadian Centre for DNA Barcoding, at the University of Guelph, Canada, for DNA extraction, amplification, and Sanger sequencing of the cytochrome *c* oxidase subunit I gene (COI), using standardized protocols (Hajibabaei et al. 2005). COI barcode compliant sequences that were generated were deposited in Barcode of Life Database (BOLD: ETKM078–ETKM083). Additional COI sequences for another 27 *Gastrocopta* specimens, belonging to 16 species derived from the studies of Nekola et al. (2012) and Whisson and Köhler (2013) were downloaded from GenBank.

Sequences were aligned using Clustal X in Bioedit V7.0 (Hall 2004). All alignments were manually optimized to ensure homology. Maximum likelihood phylogenies were inferred using Garli 2.01 (Zwickl 2006). The best-fit substitution model was estimated using JmodelTest 2 XSEDE v2.1.6 (Darriba et al. 2012). Branch-support was assessed using 1000 bootstrap replicates. A consensus tree was created from the bootstrap replicates using Phylip 3.69 (Felsenstein 2005). Trees were viewed using the program Figtree 1.3.1 (Rambaut 2009). The maximum likelihood phylogenies were midpoint rooted as no outgroups were included. Bootstrap values were annotated onto the most likely tree.

Results

Morphological characters and species identification

Shell of a honey-brown colour and moderately large (Figure 1; length of individuals with mature apertural dentition 2.3–2.7 mm), with approximately

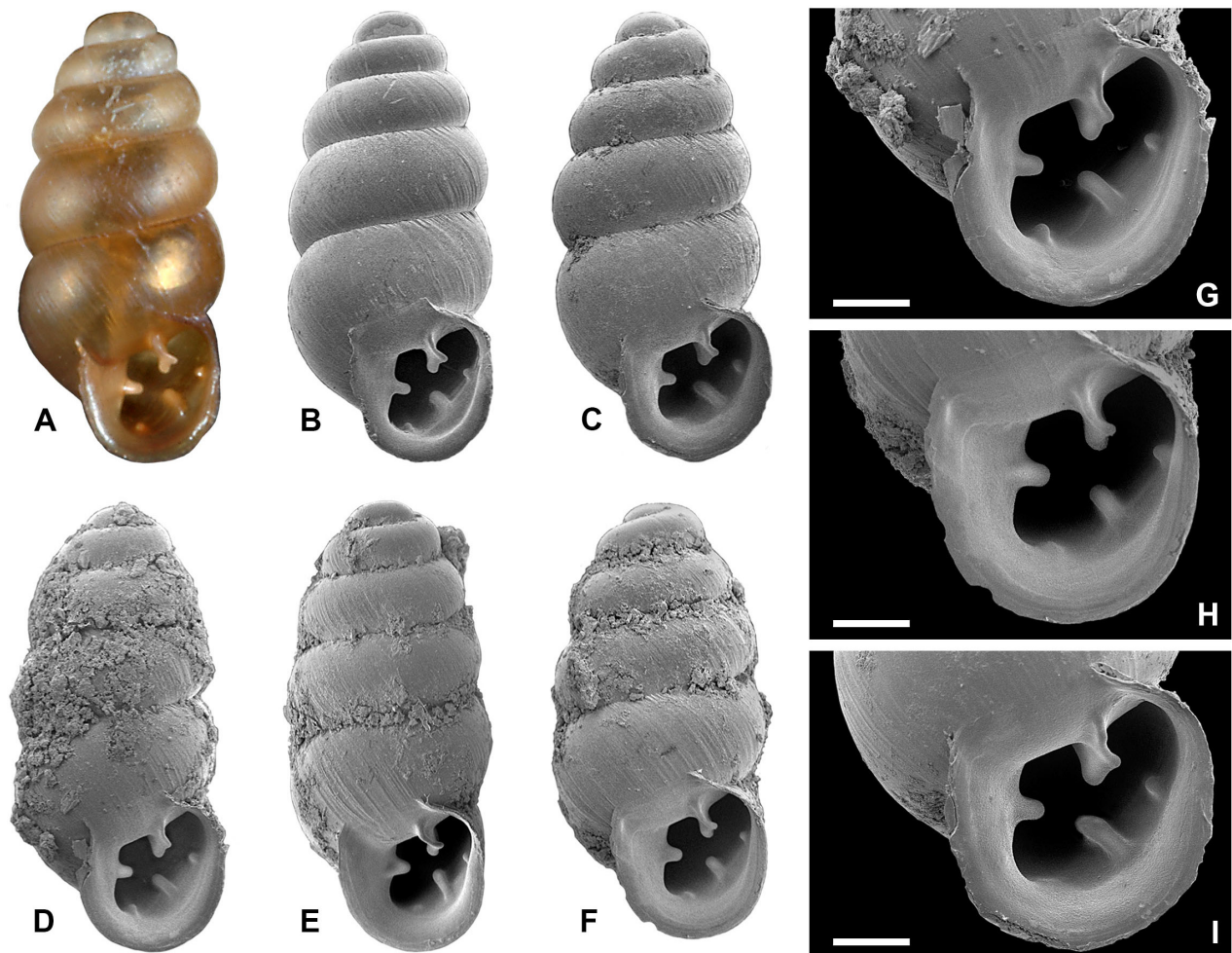


Figure 1. *Gastrocopta servilis* (Gould, 1843), Burman Bush, Durban, South Africa. Specimens showing variation in strength of the basal apertural denticle, ranging from distinct (B, D, G) to weak (A, E, F, H) to scarcely evident (C, I); specimens also vary in the extent to which the shell is encrusted with soil particles. Length (A) 2.5 mm; (B) 2.7 mm; (C) 2.44 mm; (D) 2.51 mm; (E) 2.47 mm; (F) 2.33 mm Scale bars = 250 μ m.

five whorls. The spire profile tapers gently toward the apex and whilst the whorls are distinctly convex, the suture is not particularly deeply indented. The superficial sculpture is weak, comprising only microscopic collabral growth-lines; there are no raised axial threads and no spiral sculpture. The peristome is likewise brownish and is clearly interrupted in the parietal region; the aperture lip is strongly flared and slightly thickened. Internally, the aperture has four- or five-fold dentition (Figure 1), including a horizontal lamella-like columellaris and a long, almost vertical parieto-angularis, the outer part of which is twisted toward the outer lip. In addition, there are two inset palatal denticles, the lower of which is distinctly larger, and finally a basal denticle, which though small, is clearly present in most individuals, but weak or even scarcely evident in others, even when the aperture lip is fully developed. In living specimens the shell is encrusted to a variable extent with soil particles.

When compared to indigenous dextral *Gastrocopta* species recorded from KwaZulu-Natal, namely *G. damarica* (Ancey, 1888) and *G. thomasseti* Pilsbry, 1929 (Herbert and Kilburn 2004), the Durban shells are smoother,

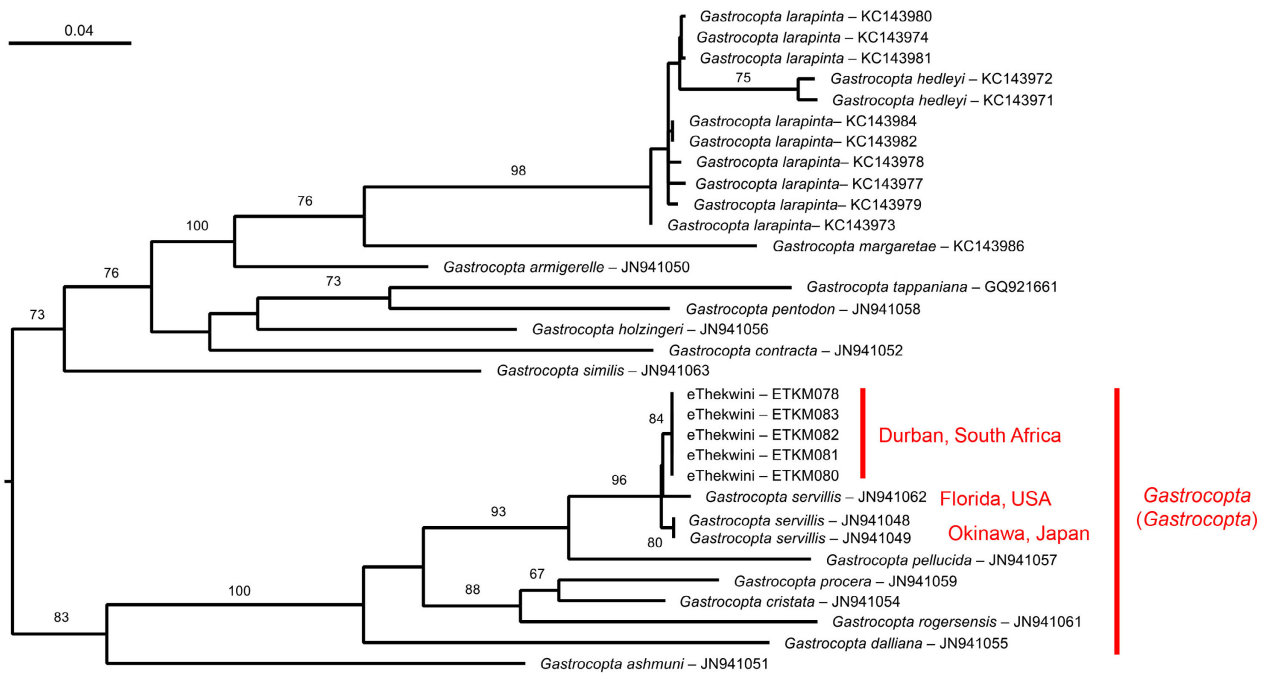


Figure 2. Mid-point rooted maximum likelihood CO1 phylogeny showing the relationship of the Durban *Gastrocopta* specimens to a range of congeneric taxa belonging to *Gastrocopta s.l.* BOLD or GenBank numbers are provided. Values on branches indicate bootstrap values. Only bootstrap values $\geq 65\%$ are provided.

have less strongly convex whorls and are generally of a larger size (max. length 2.7 mm vs. 2.3 mm). In *G. damarica*, which also has five-fold apertural dentition, the teeth are stronger and the peristome is almost complete. Since the likelihood of the Durban specimens representing an undescribed indigenous species was highly unlikely (see above) further morphological comparison focussed on gastrocoptid snails from other parts of the world, known to be proficient travellers (Robinson 1999). Through such comparison we concluded with reasonable confidence that the Durban snails could be identified as *Gastrocopta servilis* (Gould, 1843). Details of shell size, shape, colour and sculpture, as well as apertural barrier number, position and morphology are fully consistent with those of *G. servilis*, as is the fact that the palatal denticles are not borne on a callous ridge and there is no crest behind the outer lip.

Molecular confirmation of species identification

The CO1 dataset included five sequences from five individuals from the Durban population, plus 27 sequences belonging to 16 *Gastrocopta* species derived from the studies of Nekola et al. (2012) and Whisson and Köhler (2013). The maximum likelihood phylogeny (Figure 2) clearly shows that the five Durban specimens are genetically very similar, suggestive of a single colonization event, and that they are sister to *Gastrocopta servilis* from Florida. In turn, these form a sister group to *G. servilis* from Japan. The Durban specimens thus cluster within a well-supported *G. servilis* clade, providing strong evidence in support of our morphology-based identification. The *G. servilis* clade, together with *G. cristata* (Pilsbry and

Vanatta, 1900), *G. pellucida* (L. Pfeiffer, 1841), *G. procera* (A. Gould, 1840) and *G. rogersiana* Nekola and Coles, 2001, all belonging to *Gastrocopta* (*Gastrocopta*), form a strongly supported clade with *G. dalliana* (Sterki, 1898). The latter is traditionally considered to belong to *Gastrocopta* (*Immersidens*) and should group with the type species thereof [*G. ashmuni* (Sterki, 1898)]. Its anomalous position in *Gastrocopta* (*Gastrocopta*) has already been discussed by Nekola et al. (2012). The other main branch of the CO1 phylogeny includes the type species of the subgenera *G. (Albinula)* [*G. contracta* (Say, 1822)], *G. (Vertigopsis)* [*G. pentodon* (Say, 1822)], *G. (Sinlbinula)* [*G. armigerella* (Reinhardt, 1877)] and the Australian *G. (Australbinula)* [*G. hedleyi* Pilsbry, 1917].

Taxonomic summary

***Gastrocopta servilis* (Gould, 1843)**

Pupa servilis Gould, 1843: 356, pl. 16, fig. 14; Johnson 1964: 148. Type loc.: Santa Cruz and near Matanzas, Cuba.

Pupa microsoma Tapparone-Canefri, 1883: 107, pl. 2 figs 1, 2. Type loc.: Wokan, Aru Is, Indonesia.

Pupa lyonsiana Ancey, 1892: 713. Type loc. Punahou, Oahu, Hawaii.

Gastrocopta servilis; Pilsbry 1916 in 1916–1918: 70, pl. 14, figs 4–7 [1917]; Solem 1961: 447; Solem 1964: 133; Solem 1978: 42; Hubricht 1985: 9, map 58; Solem 1988: 483; Cowie 1997: 28; Vermeulen and Whitten 1998: 79, fig. 63; Bieler and Slapcinsky 2000: 15, fig. 6; Cowie 2000: 168; Rosenberg and Muratov 2006: 140, 151; Wu et al. 2007: 148; Brook 2010: 186; Stanisic et al. 2010: 104, No 123; Brodie and Barker 2011: 35; Whisson and Köhler 2013: 32, fig. 2g; Nurinsiyah et al. 2016: 559; Stanisic et al. 2018: 70, No 42; Gittenberger et al. 2019: 367; Chan and Lau 2020: 192; Espinosa and Robinson 2021: 117.

Vertigo shimochii Kuroda and Amano in Kuroda, 1960: 77, pl. 2, fig. 14; Nekola et al. 2012. Type loc.: Okinawa Is., Japan.

Distribution (Figure 3): Considered to be native to the Caribbean and Central America; introduced to many islands in the western Pacific and S-E Asia, as well as much of northern Australia, and the Maldives in the central Indian Ocean (see references in chresonymy above). Here recorded also from the eastern seaboard of KwaZulu-Natal, South Africa.

Habitat: Generally considered to be a calciphile (Hubricht 1985; Vermeulen and Whitten 1998), occurring mostly in coastal regions and preferring open grassy habitats including lawns, roadside and railway verges, and cliff tops. Solem (1988) reported it to be extremely common in port and plantation areas throughout much of the Pacific. Recorded in Australia from urban areas, plantations and other disturbed habitats (Stanisic et al. 2010, 2018). Similar habitat preferences are evident for the KwaZulu-Natal samples, except that there is no particular association with calcium-rich soils.

Date of introduction to South Africa: Prior to 1996 when the first material was collected in beach-drift at the mouth of the Mtamvuna River.

Locality data (all KwaZulu-Natal): Empangeni, edge of town (28.45°S; 31.52°E), transformed grassland, occasionally flooded by stream, leg. P. Reavell, 28/ii/2004 (NMSA W1757); Durban, Burman Bush, near scout camp

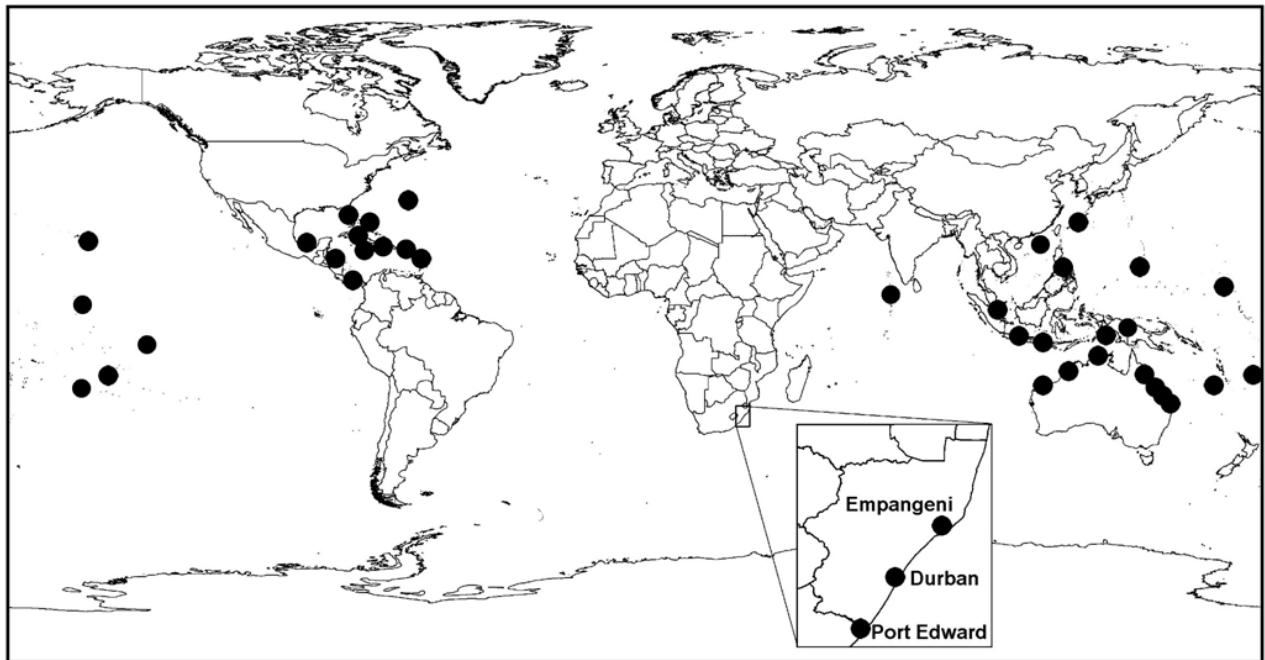


Figure 3. Global distribution of *Gastrocopta servilis*. Records sourced from references cited in chresonymy. Box represents enlargement of KwaZulu-Natal province showing new records from South Africa.

(29.8149°S; 31.0174°E), 75 m, abundant in accumulations of leaf-litter at roadside, leg. D. Herbert and L. Davis, 29/iii/2011 (NMSA W7888); Port Edward area, Mtamvuna River mouth (31.083°S: 30.197°E), beach-drift, leg. J.P. Marias, 06/i/1996 (NMSA V4029).

Discussion

The widely dispersed tropical species *Gastrocopta servilis*, known variously as the “glossy pupa snail”, “wandering snag snail” or “wandering snaggletooth snail”, is here recorded for the first time from the African continent. It represents the second tropical tramp species to be documented from the subtropical eastern seaboard of South Africa, the other being *Bradybaena similaris* (Férussac, 1822) (Herbert 2010). Currently, it is known in South Africa only from three widely separated localities in KwaZulu-Natal, but it almost certainly occurs at additional intervening sites. Due to its small size, it would be overlooked without careful scrutiny and sieving of leaf-litter. At the Burman Bush locality, a disturbed remnant of coastal bush not far from central Durban, the species is abundant in leaf-litter around and under roadside vegetation. At Empangeni it was perhaps introduced via the horticulture trade or the sugar cane and sylviculture industries. The material collected at the mouth of the Mtamvuna River was almost certainly washed downstream, perhaps from the sugar cane or banana plantations in the lower catchment.

Whereas *G. servilis* is widespread in the western Pacific and S-E Asia, and has been so since before 1900, the present record is the first for Africa. In reality, however, the species may also have been present in the south-western Indian Ocean prior to 1900. A number of species described from

the islands of the south-western Indian Ocean bear a very close resemblance to *G. servilis*. These include *Gastrocopta microscopica* (von Martens, 1898) described from the Seychelles, as well as *G. lienardiana* (Crosse, 1873) from Rodrigues, *G. madagascariensis* (Bavay and Germain, 1920) and *G. seignaciana* (Crosse and Fischer, 1879) from Madagascar, and *G. tripunctum* (Morelet, 1882) from Mayotte. Pilsbry (1917 in 1916–1918: 119, 127) noted the similarity between *Gastrocopta* species from the Antilles and some African and Mascarene species stating “they are so closely interrelated that one is inclined to think them local races of a single species, which may have been carried about on plants within the period of human occupation. The resemblance to the equally widespread Antillean species *G. servilis* is very close”. However, he hesitated to conclude that any of these south-western Indian Ocean species represented introduced populations of Antillean origin. Adam (1954) similarly considered the *Gastrocopta* species of the Indian Ocean islands to be very similar to each other and to *G. servilis*, but his conclusions were likewise not definitive.

Given the ease with which small snails can be translocated and the extent to which *G. servilis* has colonised islands in S-E Asia and the western Pacific, we consider it probable that the same has happened on the islands of the western Indian Ocean and on its continental margin. Here, as in the western Pacific, the introduced populations have frequently been redescribed as supposedly indigenous species – the pseudoindigenes of Carlton (2009). Fischer-Piette et al. (1994) have already relegated *G. tripunctum* and *G. madagascariensis* to the synonymy of *G. seignaciana*, and Gerlach (2006) considered this in turn to be the same as *G. microscopica* (though he incorrectly credited the latter name to Nevill, 1878 and thus afforded it priority). Molecular data for these Indian Ocean island populations will be needed in order to explore this hypothesis more fully and to test whether they all originate from introductions of *G. servilis*. On the available morphological evidence we consider this a strong possibility. Verdcourt (2007) has similarly recorded the Caribbean *G. pellucida* (L. Pfeiffer, 1841) as an introduction in Ghana.

Brodie and Barker (2011) assessed the potential risks associated with introduced land snails in the Fijian Islands and concluded that *Gastrocopta servilis*, being a detritivore, was likely to be of low pest-risk, but that it may compete with indigenous micro-snails in leaf-litter habitats. Cowie (1997) noted that the species was now a dominant member of lowland land snail communities in Hawaii. It thus has the potential to invade and impact such communities in coastal KwaZulu-Natal. Further risks may involve the transmission of snail-borne diseases and non-native parasites (Lu et al. 2018).

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Author's contribution

DGH was responsible for sample collection; project conceptualization; morphological investigation, analysis and interpretation of data; drafting initial manuscript. SW-M was responsible for DNA sequencing and analyses; interpretation of molecular data; drafting the related sections of the manuscript.

Ethics and permits

Samples were collected under a permit provided by Ezemvelo KwaZulu-Natal Wildlife (Permit No 4674).

References

- Adam W (1954) Études sur les mollusques de l'Afrique centrale et des régions voisines 1. Vertiginidae et Valloniidae. Volume Jubilaire Victor Van Straelen. Tome II. Institut Royal d'Histoire Naturelle de Belgique, Brussels, pp 725–817
- Ancey CMF (1892) Étude sur la faune malacologique des Iles Sandwich. *Mémoires de la Société zoologique de France* 5: 708–722
- Bieler R, Slapcinsky J (2000) A case for the development of an island fauna: Recent terrestrial mollusks of Bermuda. *Nemouria (Occasional Papers of the Delaware Museum of Natural History)* 44: 1–99
- Brodie G, Barker GM (2011) Introduced land snails in the Fiji Islands: are there risks involved? In: Veitch CR, Clout MN, Towns DR (eds), *Island invasives: eradication and management*. IUCN, Gland, Switzerland, pp 32–36
- Brook FJ (2010) Coastal landsnail fauna of Rarotonga, Cook Islands: systematics, diversity, biogeography, faunal history, and environmental influences. *Tuhinga* 21: 161–252
- Carlton JT (2009) Deep invasion ecology and the assembly of communities in historical time. In: Rilov G, Crooks JA (eds), *Biological invasions in marine ecosystems*. Ecological Studies, 204. Springer-Verlag, Berlin, pp 13–56, https://doi.org/10.1007/978-3-540-79236-9_2
- Chan S-Y, Lau WL (2020) New record of glossy pupa snail, *Gastrocopta servilis*, in Singapore. *Singapore Biodiversity Records* 2020: 192–195
- Connolly M (1939) A monographic survey of South African non-marine Mollusca. *Annals of the South African Museum* 33: 1–660
- Cowie RH (1997) Catalog and bibliography of the nonindigenous nonmarine snails and slugs of the Hawaiian Islands. Bishop Museum, Occasional Papers No 50, 66 pp
- Cowie RH (2000) Non-indigenous land and freshwater molluscs in the islands of the Pacific: conservation impacts and threats. In: Sherley G (ed), *Invasive species in the Pacific: a technical review and draft regional strategy*. South Pacific Regional Environment Programme, Samoa, pp 143–172
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9: 772, <https://doi.org/10.1038/nmeth.2109>
- Espinosa JA, 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>
- Felsenstein J (2005) PHYLIP (Phylogeny Inference Package) version 3.6. Department of Genome Science, University of Washington, Seattle
- Fischer-Piette E, Blanc CP, Blanc F, Salvat F (1994) Faune de Madagascar. 83. Gastéropodes terrestres pulmonés. Muséum National d'Histoire Naturelle, Paris, 551 pp
- Gerlach J (2006) Terrestrial and freshwater Mollusca of the Seychelles Islands. Backhuys, Leiden, 141 pp
- Gittenberger E, Reijnen BT, Groenenberg DSJ (2019) Terrestrial gastropods of the Maldives, all of which are invasive? *Journal of Conchology* 43(4): 353–383
- Gould AA (1843) Monograph of the species of *Pupa* found in the United States. *Boston Journal of Natural History* 4: 350–360, <https://doi.org/10.5962/bhl.part.16997>
- Hajibabaei M, Dewaard JR, Ivanova NV, Ratnasingham S, Dooh RT, Kirk SL, Mackie PM, Hebert PD (2005) Critical factors for assembling a high volume of DNA barcodes.

- Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 1959–1967, <https://doi.org/10.1098/rstb.2005.1727>
- Hall T (2004) BioEdit version 7.1.11. Department of Microbiology, North Carolina State University, USA, <http://www.mbio.ncsu.edu/BioEdit/bioedit.html>
- Herbert DG (2010) The introduced terrestrial Mollusca of South Africa. SANBI Biodiversity Series 15. South African National Biodiversity Institute, Pretoria, 108 pp
- Herbert D, Kilburn D (2004) Field guide to the land snails and slugs of eastern South Africa. Natal Museum, Pietermaritzburg, 336 pp
- Hubricht L (1985) The distribution of the native land molluscs of the eastern United States. *Fieldiana: Zoology* 24: 1–191, <https://doi.org/10.5962/bhl.title.3329>
- Johnson RI (1964) The Recent Mollusca of Augustus Addison Gould. Smithsonian Institution, Washington. 182 pp, 42 pls, <https://doi.org/10.5479/si.03629236.239>
- Kuroda T (1960) A Catalogue of Molluscan Fauna of the Okinawa Islands (exclusive of Cephalopoda). Ryukyu University Publications, Okinawa, 106 pp, 3 pls
- Lu XT, Gu QY, Limpanont Y, Song LG, Wu ZD, Okanurak K, Lv ZY (2018) Snail-borne parasitic diseases: an update on global epidemiological distribution, transmission interruption and control methods. *Infectious Diseases of Poverty* 7: 28, <https://doi.org/10.1186/s40249-018-0414-7>
- Nekola JC, Jones A, Martinez G, Martinez S, Mondragon K, Lebeck T, Slapcinsky J, Chiba S (2012) *Vertigo shimochii* Kuroda & Amano, 1960 synonymized with *Gastrocopta servilis* (Gould, 1843) based on conchological and DNA sequence data. *Zootaxa* 3161: 48–52, <https://doi.org/10.11646/zootaxa.3161.1.4>
- Nurinsiyah AS, Fauzia H, Hennig C, Hausdorf B (2016) Native and introduced land snail species as ecological indicators in different land use types in Java. *Ecological Indicators* 70: 557–565, <https://doi.org/10.1016/j.ecolind.2016.05.013>
- Pilsbry HA (1916-1918) Pupillidae (Gastrocoptinae). Manual of Conchology. Second series, vol. 24: 1-380. Academy of Natural Sciences, Philadelphia, pp 1-112, 1916; 113-256, 1917; 257-380, 1918; pls 1-13, 1916; pls 14-38, 1917; pls 39-49, 1918
- Rambaut A (2009) FIGTREE. <http://tree.bio.ed.ac.uk/software/figtree/>
- Robinson DG (1999) Alien invasions: the effects of the global economy on non-marine gastropod introductions into the USA. *Malacologia* 41(2): 413–438
- Rosenberg G, Muratov IV (2006) Status report on the terrestrial Mollusca of Jamaica. *Proceedings of the Academy of natural Sciences, Philadelphia* 155: 117–161, <https://doi.org/10.1635/i0097-3157-155-1-117.1>
- Solem A (1961) New Caledonian land and freshwater snails. An annotated check list. *Fieldiana: Zoology* 41: 413–501, <https://doi.org/10.5962/bhl.title.2941>
- Solem A (1964) New records of New Caledonian nonmarine mollusks and analysis of the introduced mollusks. *Pacific Science* 18: 130–137
- Solem A (1978) Land snails from Mothe, Lakemba, and Karoni Islands, Lau Archipelago, Fiji. *Pacific Science* 32(1): 39–45
- Solem A (1988) Non-camaenid land snails of the Kimberley and Northern Territory, Australia. I. Systematics, affinities and ranges. *Invertebrate Taxonomy* 4: 455–604, <https://doi.org/10.1071/IT9880455>
- Stanisic J, Shea M, Potter D, Griffiths O (2010) Australian land snails Vol. 1. A field guide to the eastern Australian species. Bioculture Press, Mauritius, 591 pp
- Stanisic J, Shea M, Potter D, Griffiths O (2018) Australian land snails. Vol. 2. A field guide to southern, central and western species. Bioculture Press, Mauritius, 594 pp, <https://doi.org/10.17082/j.2204-1478.61.2019.2018-13>
- Tapparone-Canefri C (1883) Fauna malacologica della Nova Guinea e delle isole adiacenti. Parte I. Molluschi estramarina. *Annali del Museo Civico di Storia Naturale "Giacomo Doria"* 19: 1–313
- Verdcourt B (2007) Miscellaneous notes on tropical African non-marine Mollusca. *Annales Historico-Naturales musei Nationalis Hungarici* 99: 189–197
- Vermeulen JJ, Whitten AJ (1998) Fauna Malesiana. Guide to the land snails of Bali. Backhuys, Leiden, 164 pp
- Whisson CS, Köhler F (2013) *Gastrocopta* (Mollusca, Gastropoda, Pupillidae) in the Pilbara region of Western Australia. *ZooKeys* 261: 15–39, <https://doi.org/10.3897/zookeys.261.4269>
- Wu S-P, Hwang C-C, Huang H-M, Chang H-W, Lin Y-S, Lee P-F (2007) Land molluscan fauna of the Dongsha island with twenty new recorded species. *Taiwania* 52(2): 145–151
- Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD thesis, University of Texas, Austin, USA, 115 pp