Comparative analysis of wild and long term captive bred *Partula* snails using morphometrics and population data.

Volume 1

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Master's in Philosophy

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2021

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iv. Acknowledgements

I would first like to thank my supervisors, Dr Rachael Antwis and Dr Chiara Benvenuto for giving me their time, support, and encouragement, even when things didn't go to plan! A sincere thank you to Paul Pearce-Kelly, Dave Clarke, and Elaine Brown at ZSL London. Paul thank you for giving me the opportunity to complete this research project and work with you and your team. The time that you have all given, the introductions to other scientists and organisations, advice, guidance, and support throughout this project has been invaluable. Dave thank you for your support and guidance with the snails and the extraction of data from the database. Elaine thank you for providing such detailed specimen information and support with the data extraction. I would also like to extend a thank you to you and all your colleagues in BUGS for welcoming me during my visits. Thank you to Jon Ablett at Natural History Museum for being so welcoming and giving me time to train me in the use of digital calipers. A personal thank you to my husband, Neil and our son, Austin for their unwavering and continuous support and encouragement. Neil I will always be grateful to you for letting me take the time out of busy family and working life to complete this research project, I hope this achievement will contribute to a bright a successful future for us. Thank you for all my family and friends for their support in all areas to help me complete this project. Without the support of all these people I would not be where I am now, so thank you all.

v. Statement of Originality

I declare that, with the exception of any statements to the contrary, the contents of this report/dissertation are my own work, that the data presented herein gas been obtained by experimentation and that no part of the report has been copied from previous reports/dissertations, books, manuscripts, research papers or the internet.

Signed: ____________________________ Print Name: ____________________________

Date: _____________________________

vi. Abbreviations

CR	Critically endangered
CVA	Canonical variate analysis
EX	Extinct
EW	Extinct in the wild
F01	Founding first generation
F02	Founding second generation
F03	Founding third generation
F04	Founding fourth generation
F05	Founding fifth generation
F06	Founding sixth generation
F07	Founding seventh generation
F08	Founding eight generation
F09	Founding ninth generation
F10	Founding tenth generation
F11	Founding eleventh generation
IUCN	International Union for Conservation of Nature
NA	Data not available
PCA	Principal component analysis
Par	Wild specimens
P	Wild specimens
*P*GSMP	*Partulid* Global Species Management Programme
*P*SMP	*Partulid* Species Management Programme
VU	Vulnerable
ZSL	Zoological Society of London

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vii. Abstract

Partula snails are one genus of the Partulidae family of air breathing, land snails that are endemic to the Pacific Islands. Over 100 partulid species are recognised with over half these species known to have existed and endemic to the Society Islands (within the Pacific islands). It is thought that 56 of these endemic *Partula* species are now extinct on the Society Islands with the remaining species critically endangered. This devastating extinction is mainly the result of the introduced carnivorous rosy wolf snail, *Euglandina rosea* in 1974. The most imposing threat today is the introduced New Guinea flatworm, *Platydemus manokwari.* To save the remaining *Partula* species from extinction, specimens have been collected since 1962 to start a captive breeding programme coordinated by the Zoological Society of London (ZSL). Over 15 species are kept in captivity currently. Several reintroductions have taken place with over 10,000 snails being reintroduced to the islands with varying levels of success. *Partula* have been in captivity now for over 60 years, with many of the species founded with small numbers. There is concern about how this species may be adapting morphologically to their captive environment as they are known to be sensitive to environmental changes. This study focused on ten species of *Partula* with multiple generations in captivity, which made it possible to compare the morphology of wild to captive-bred specimens. The study found that seven of the ten species displayed no significant morphological changes during long-term captivity (*P. clara, P. garrettii, P. hebe bella, P. otaheitana, P. rosea, P. suturalis strigosa* and *P. varia*). Three species did show significant morphological changes at various stages throughout captivity. The morphological changes that *P. faba* displayed were likely adaptations to its captive environment. *Partula faba* did not survive in captivity as a result of the low genetic diversity within the captive population due to the depleted wild population. *Partula affinis* appears to have gradually changed morphologically to presumably adapt to the captive environment. *Partula tohievana* displayed morphological changes between two generations only, suggesting a local

mutation event caused by low genetic diversity. This species should be monitored in captivity as it may suffer a similar fate to *P. faba* and face extinction in captivity. Overall, long-term captivity does not appear to have negatively affected the morphology of *Partula* and therefore suggests positive outcomes for future reintroductions.

1. Introduction

1.1. *Partula* snail natural history

Partula snails are one genus of the Partulidae family of air breathing, land snails that are endemic to the Pacific islands (Figure 1), often referred to as the Polynesian tree snail (Gouveia, 2011). There are two other genera that belong to the Partulidae family: *Eua* and *Samoana* (Cowie, 1992), however for the purpose of this study the focus is *Partula* snails. Figure 2 shows an image of the *Partula taeniata,* which is now believed to be extinct in the wild (Coote & Loeve, 2003). *Partula* snails were first described during Captain Cook's voyage in 1774 (Pearce-Kelly *et al.,* 2006). A recent phylogeny suggests that *Partula* evolved approximately 3.6 million years ago, and two main clades have been identified, Western and Eastern (Lee, Churchill & O'Foighil*.,* 2014; Figure 1).

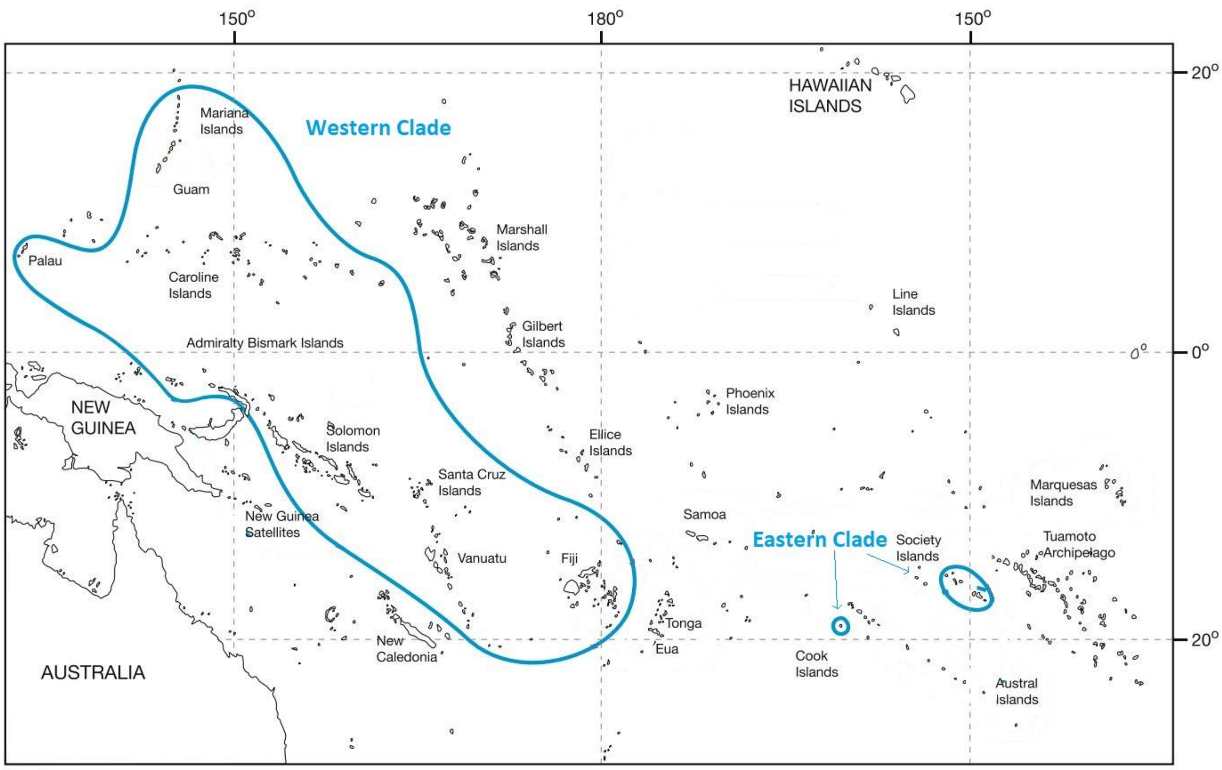


Figure 1. *Partula* distribution within the Pacific islands. Map modified from Lee *et al.,* 2014.

Approximately 120 partulid species are recognised with over 60 of these species known to have existed and been endemic to the Society Islands in the Eastern clade (Lee *et al.,* 2014 & Haponski, Taehwan & O'Foighil*.,* 2017) on the islands of Bora Bora, Huahine, Raiatea, Tahea, Moorea and Tahiti (Figure 2; Coote & Loeve, 2003). It is thought that 56 of these endemic *Partula* species are now extinct on the Society Islands (Coote & Loeve, 2003). According to available data, there are five *Partula* species that survive on the Society Islands: *P. affinis, P. clara, P. hyalina. P. mirabilis* and *P. otaheitana*, (Coote & Loeve, 2003), but all of these are critically endangered with extremely small and isolated populations (IUCN, 2019a).

Figure 2. Image of *Partula taeniata*, critically endangered with an estimated population between 10 and 100 mature individuals remaining in the wild (IUCN, 2019a).

Partula snails are small, growing up to 2cm in length (ZSL, 2019). They are estimated to live up to 10 years depending on the species (Clarke, 2019). Several of the species have a varying number of colour morphs and banding on the shell that have been present in wild populations (Gouveia, 2011; see Appendix 1 for information found on colour morphs that have been recorded). They are mainly nocturnal/crepuscular (Murray, Johnson & Clarke*.,* 1982) and are generally found in high volcanic or coral islands with a constant high temperature and humidity with two distinct seasons (Gouveia, 2011). The snails can also be classified into three different habitat types: ground-dwelling, semi arboreal and arboreal. The ground dwelling species stay on the ground hiding under stones, dead leaves, and trees, whereas the semi-arboreal species remain under leaves and sealed during the daytime up to five metres above the ground and come down to the ground at dusk to feed. The arboreal species are strictly arboreal spending their whole life in the trees (Crampton, 1916). All *Partula* species have been described as detritivores (Coote, 2007), however in a collation of data available species have been categorised into dietary preferences: detritivore, fungivore or herbivore. A species is described as a specialist if the gut content showed >90% of one particular dietary category or a generalist if the gut content was between 50-90% (Gerlach, 2016).

Partula snails are cross-fertilising hermaphrodites (Clarke, 2019) self-fertilisation is rare (Murray & Clarke, 1966) although has been observed in captivity even when some species of *Partula* have been paired (Gerlach, 2016). Sperm can be stored for up to two years for *P. suturalis* (Davidson *et al.,* 2009), however for other species sperm storage duration is far less (Gerlach, 2016). They are ovoviviparous, which means they produce young from eggs which are hatched within the body of the parent, giving birth predominately to a single shelled snail every six to eight weeks (Gouveia, 2011), twins can be born occasionally (Gerlach, 2016). Maturity is reached between three to six months (Johnson, Murray & Clarke., 1993). The gestation period is approximately three months, however young at different development stages maybe present in the oviduct at any one time. This means that the snails can have an average reproduction rate of one birth per month (Murray & Clarke., 1984). Reproduction is generally all year round, however it could be influenced by season. Four distinct development stages are recognised in snail growth; new born which is any snail >5mm, juvenile, sub adult and adult. Adults are fully mature snails, the only stage that is reproductive and adults are recognised by the thickened edge to the shell aperture, known as the lip (Clarke, 2019).

Partula snails, like all gastropods, have an ecological importance for the environment that they live in. They help keep the environment clean of organic dead or decaying matter and recycle nutrients back into the environment (Barker, 2001). These snails also hold particular social and economic value for the local artisan community. Women would make *lei* (jewellery) from the shells, and as such, the decline and extinction of the snails has led to losses for the local communities (Coote & Loeve, 2003).

1.2. Extinction crisis

Partula snails have few natural predators including birds and lizards, and the Polynesian women that used to collect the shells to create *'lei'* jewellery to sell (Clarke, 2019).

However, the extinction of the *Partula* snail has mainly been due to a poorly planned introduction of an invasive species, the rosy wolf snail; *Euglandina rosea* (Coote & Loeve, 2003). The rosy wolf snail was first introduced in Tahiti in 1974, in Moorea in 1977 and then in the other Society Islands in the 1980s and 1990s (Coote, 2007). The aim of the predatory snail introduction was to control the introduced population of the giant African land snails, *Achatina fulica*, which were brought to the islands as a food source in 1967 (Coote *et al.,* 1999). The *A. fulica* were subsequently released or escaped into the wild and started to decimate crops (Clarke, Murray & Johnson*.,* 1984; Murray *et al.,* 1988; Cowie, 1992). The rosy wolf snail has had devasting effects on the *Partula* snail species living on the islands and is responsible for the extinction of 56 of the 61 *Partula* species (Table 1; Coote & Loeve, 2003), that is 92% of the *Partula* species. The predator targets the native snail species by following the mucus trail left behind and then consuming its prey whole or piecemeal (Gerlach, 2001). It is believed that a small number of Moorean and Tahitian species of *Partula* snail continue to exist on the islands, high up in the montane cloud forests >1000m, where the predator *E. rosea* is not so successful (Haponski *et al.,* 2016) and in the valleys of Tahiti and Moorea (Coote, 2007 & Lee *et al.,* 2009). The two species to survive in the Tahiti valleys are *P. hyalina* and *P. clara* (Coote, 2007), where they have managed to survive over 40 years of predation from *E. rosea* (Gerlach, 2001). Their survival is due to a higher fecundity compared to co-occurring congeners (Bick *et al.,* 2016 & Bick *et al.,* 2018). The only islands where *E. rosea* has not yet been found is the Marquesas, North West of the Society islands in the Eastern clade, where seven Partulidae species exist (Coote & Loeve, 2003).

The second invasive species that also has contributed to the decline and extinction of the *Partula* snail is the New Guinea flatworm, *Platydemus manokwari* (Gerlach, 2016), which feed on the *Partula* snails and also on *E. rosea* (Gerlach, 2016). The survival of the *Partula* snail is also threatened by other factors including climate change and possibly the newly discovered predatory ribbon worm, *Geonemertes pleaensis*. Although small populations of *Partula* may survive in the cloud forests >1000m where *E. rosea* are rarely found, increases in global temperatures may mean these higher altitude areas become suitable habitat for the invasive species, which would lead to potentially devastating effects for the surviving *Partula* species (Gargominy, 2008). Habitat loss and alteration and small extant population sizes are also factors that are threatening the survival of *Partula* (Sakamoto, 2016). However, it appears the priority in terms of conservation efforts is the control of *E. rosea* to secure a future for the *Partula.*

Table 1. Species of *Partula* snail that existed on the Society Islands, and those that are now extinct (Coote & Loeve, 2003). The species with a * have wild specimens to compare with captive bred specimens for the purpose of this study.

	Society Islands						**Extinct in the wild**
Species	**Bora Bora**	**Huahine**	**Raiatea**	**Tahaa**	**Moorea**	**Tahiti**	
Partula							
P. affinis *						√	
P. arguta		√					√
P. atilis			√				√
P. aurantia					√		√
P. bilineata				√			√
P. candida			√				√
P. citrinin			√				√
P. clara *						√	
P. crassilibris			√				√
P. cytherea						√	√
P. dentifera			√				√
P. dolorosa			√				√
P. eremita				√			√
P. exigua					√		√
P. faba *			√				√
P. filose						√	√
P. formosa			√				√
P. fusca			√				v
P. garretti *			√				√
*P. hebe bella**			√				√
P. hyalina						√	
P. imperforata			√				√
P. labrusca			√				√
P. leptochila			√				√
P. levilineata			√				√
P. lugubris			√				√
P. lutea	√						√
P. mirabilis					√		
P. mooreana					√		√
P. navigatoria			√				√
P. nodosa						√	√
P. otaheitana *						√	
P. ovalis			√				√
P. planilabrum				√			√
P. producta						√	√
P. radiata			√				√
P. remota			√				√

P. robusta			√				√
*P. rosea **		√					√
P. rustica			√				√
P. sagitta				√			√
P. subangulata				√			√
*P. suturalis **					√		√
P. taeniata					√		√
P. thalia			√				√
*P. tohiveana **					√		√
P. tristris			√				√
P. turgida			√				√
P. umbilicata				√			√
*P. varia **		√					√
P. vittate			√				√
P. X callifera			√				√
P. X cedista			√				√
P. X cuneara			√				√
P. X dolichostoma			√				√
P. X levistriata			√				√
P. X protracta			√				√

1.3. Conservation Efforts

Living specimens of *Partula* snails have been collected on various expeditions to the French Polynesia since 1962 and kept in collections in Europe, USA, and Australia (Gouevia, 2011). In 1986 the International *Partula* Breeding Programme was created with the aim of securing a future for this severely threatened group through captive breeding programmes and possibly reintroduction into the wild (Tudge & Pearce-Kelly, 1992 & Clarke, 2019). Several expeditions to the French Polynesia were made during the 1990s and early 2000s to survey the islands by measuring the impact of *E. rosea* and to collect *Partula* specimens for the captive breeding programme. In 1991, 'Operation *Partula*' was launched to measure the status of *Partula* and *E. rosea* on the Society Islands. Only dead *Partula* shells were found on Moorea, but rescue collections were made on Raiatea and on Huahine. A one-day survey of Bora Bora reported an extinction of the species (Coote & Loeve, 2003). In 1992, further surveys of Raiatea found *Partula* in just four locations where *E. rosea* was absent, and in other locations where both species existed (Gerlach, 1994). In 1994, further surveys of Raiatea and Tahaa found no living *Partula* and between 1992 and 1994 *E. rosea* had been introduced to Huahine and was threatening *Partula* survival (Pearce-Kelly, Mace & Clarke., 1995). By 1987, all seven of the *Partula* species on Moorea were thought to be extinct until 1998, when a small population was found (Coote, 1999). On Tahiti, several small populations of *Partula* species have been discovered (*P. affinis, P. hyalina, P. clara* and *P. otaheitana)*, mostly at altitudes above 1000m in the montane forest where access is difficult (Coote *et al.,* 1999). In 2000 and 2001, surveys on Huahine, Raiatea and Tahiti were carried out to gather information on habitat to support the captive breeding programme.

There are 16 collections worldwide that support the captive breeding programme, with the Zoological Society of London (ZSL) being responsible for the coordination. There are 11 species and four sub-species of *Partula* snail held across all the collections involved in the programme (Table 2; D. Clarke, personal communication, 2019). Each collection is advised to follow strict husbandry guidelines as *Partula* species are poikilothermic, being sensitive to slight changes in their environment including humidity and temperature (Pearce-Kelly *et al.,* 1995 & Gouveia, 2011). The current recommended housing for the snails consists of small glass tanks that have a sheet of water-soaked kitchen roll placed on the bottom to provide humidity, and a sheet of clingfilm placed tightly over the top of the tank, to help maintain humidity in the tank and to prevent snails escaping. The tanks are maintained at a temperature range of 20-24°C and 60-80% humidity, similar to wild conditions (Pearce-Kelly *et al.,* 2007). Nottingham University developed the original diet for captive snails, which has been shared with all collections (Tonge & Bloxam, 1991). The snail diet comprises of powdered cuttlebone or chalk, porridge oats, dried grass powder, powdered trout pellets, vitamin powder (SA-37 or Stress), vitamin E and water to create a paste (Tonge & Bloxam, 1991), which is smeared on to a glass plate that is placed in the tank (Pearce-Kelly *et al.,* 2007). Record keeping is vital for monitoring the captive populations: each collection records data on the species in their care and provides this data to ZSL on a regular basis, so each population can be monitored and if necessary, action taken (D. Clarke, personal communication, 2019). The information provided includes births, deaths and population counts for each life stage which is recorded on the International Partulid

Species Management System (PSMS), managed by ZSL. Over 50,000 *Partula* specimens are kept and preserved at ZSL London (E. Brown, personal communication, 2019).

Table 2. *Partula* snail species and subspecies kept in various collections and their IUCN Redlist status: EX – extinct, EW – extinct in the wild, VU – vulnerable, CR – critically endangered, ↓ – population decreasing, and NA – not available on the IUCN Redlist website.

Species & sub species	**IUCN Redlist Status**	**London**	**Chester**	**Edinburgh**	**Bristol**	**Marwell**	**Artis**	**Detroit**	**Disney**	**Dusseldorf**	**Akron**	**Sedgewick County**	**Pozan**	**Riga**	**St Louis**	**Whipsnade**	**Woodland Park**
P. navigatoria	EX	√			√												
P. hebe bella	EW	√			√												
P. hyalina	VU ↓	√				√	√										
P. mirabilis	EW	√			√								√				
P. mooreana	EW	√				√											
P. garretti	EX	√			√									√			
P. tohiveana	EW	√		√						√							
P. rosea	EW		√													√	
P. varia	EW		√			√								√			
P. affinis	CR ↓			√			√										
P. nodosa	EW						√	√	√		√	√			√		√
P. suturalis vexillum	EX	√		√												√	
P. taeniata nucleola	EX	√				√											
P. taeniata simulans	NA			√													
P. suturalis strigosa	EX				√								√	√			

1.4. Reintroductions

Reintroductions of species in the wild are becoming more common, however many still fail (Griffith *et al*., 1989; Muths, Bailey & Watry., 2014). It is suggested that failure occurs due to poor planning and implementation (Griffith *et al*., 1989), despite the IUCN producing generic guidelines for reintroductions in 1998, which were revised in 2013 (IUCN/SSC, 2013).

Captive bred *P. taeniata elongata* were released into an area of native Polynesian plants located in the north end of the Asian sector of the Palm House at the Royal Botanic Gardens, Kew (UK) in 1993. The area chosen included plants that were close relatives to those chosen by *Partula* in the wild. A group of mixed generation snails were placed in an experimental tank with an open door allowing the snails to leave the tank. The group comprised of 30 adults, 10 sub-adults and 20 juveniles. The adults were marked with identification numbers, the sub-adults and juveniles were not marked to avoid causing damage to the delicate and growing shells. A control group of snails was also set up in the release area but housed in a small, closed tank. The purpose of the control group was to monitor the background climatic effects whilst continuing with the captive husbandry protocol. Intense 24-hour monitoring of the snails at 30-minute intervals was conducted for the first two weeks after their release, with priority focused on survival rates, behaviour, and rates of dispersal. Following the initial release, monitoring was gradually reduced over the following 15 months. At the end of the first two weeks, the control tank snails were also released, and the adults marked with a colour at the tip of the shell. Results showed a minimum of 16 new-borns in the area, and several comparative wild behaviours including a low rate of dispersal and feeding on decaying plant material. These results helped to demonstrate that the captive breeding environments are suitable for the species as they allowed the species to retain natural behaviours, such as foraging and reproduction, required to survive in semi-wild environments (Pearce-Kelly *et al.,* 1995).

In 1994, the construction of a predator-proof area was built in Afareaito Valley on the island Moorea where three indigenous species of captive bred *Partula* (*P. suturalis, P.*

teaniata and *P. tohiveana*) of mixed generations were released. The research project monitored the effectiveness of physical predator exclusion methods in the form of galvanised iron roof panels and electric wiring and a chemical predator exclusion method of salt trenches. The behaviour of the captive bred snails was evaluated in the wild environment. The predator-proof area was split into four quadrants. Three quadrants received an equal number of adult individuals of a different single species and the fourth quadrant received an equal mix of all species. Each adult was marked based on the quadrant they were released into, therefore allowing the research to show habitat preference at the end of the project. Monitoring and maintenance by a third party initially proved difficult, allowing several incursions of *E. rosea* which decimated the *Partula*. Over the course of the research, a total of 320 individuals were released with only one individual of *P. taeniata* and *P. tohiveana* surviving, but a healthy population of *P. suturalis* remained. Despite the incursion of *E. rosea,* researchers did find *Partula* without identification marks indicating that the snails were capable of reproducing and three of the four possible colour morphs were seen *in P. suturalis*. These results demonstrated that after six generations in captivity, the *Partula* species had retained sufficient genetic and ecological properties to potentially survive in the wild (Coote *et al.,* 2004). In 1996 the Moorean predator proof reserve was restocked but was later ended in 1998 due to the continued difficulties with maintenance of the site. In 2002 a predator proof reserve was set in the Faaroa valley on the island of Tahiti and a secondary reserve in the Te Faaiti valley in 2012. These reserves continue to receive captive bred snails for rerelease. An experimental release of snails was also conducted on Raiatea in 2016 after finding remnant populations of *Partula* in 2006.

Initially it was thought that reintroduction of the *Partula* snail would not be successful in the short term due to the abundance and growing distribution of the predatory snail *E. rosea* in their habitat (Pearce-Kelly *et al.,* 1995). However, the captive breeding programme has seen nearly 10,000 snails reintroduced to Polynesia since 2015 (Clarke, 2019).

1.5. The effects of captivity on the snail's morphology

Reintroduction failures have also been attributed with phenotypic changes in the physiology and morphology of captive bred animals (O'Regan & Kitchener, 2005; Tarszisz, Dickman & Munn, 2014). Morphological change in captive animals may results from phenotypic plasticity (Miner *et al.,* 2005; Schulte-Hostedde, 2015), and gastropods are known to demonstrate plasticity in respect to their environment and predators (Appleton & Palmer, 1988; Trussell, 2000). Captivity is also known to drive changes in soft tissue morphology (McPhee, 2004), although this has not been explored in this study as soft tissue was not available for the most the specimens but could potentially be a future study if soft tissue is available from wild specimens for comparison with captive-bred specimens.

Some of the *Partula* snail species have been in captivity for nearly 60 years now, and any captive breeding programme needs to monitor the species closely to ensure that genetic adaption to captivity is minimised (Frankham *et al.,* 1986). Many of the species brought into captivity from the wild were in small numbers from isolated populations or for some species the last remaining known populations of the species (D Clarke. personal communication, 2021). This means that some of the species could have suffered a severe bottleneck in genetic viability (O'Regan & Kitchener, 2005).

Shell size, shape and colour are good indicators to measure for conservation as the IUCN recommends individuals selected for reintroductions must be genetically, morphologically, physiologically, and behaviourally comparable to wild populations (IUCN/SSC, 2013). It has also been shown in land snails that shell shape and size are linked to life history and fitness traits including offspring size, offspring number, and age at first reproduction (Barrientos, 1998; Anderson, Weaver & Guralnick., 2007). Sakamoto (2011) compared the effects of 25 years in captivity on the morphology of *P. rosea* and *P. varia* and found that *P. varia* displayed immediate morphological changes in captivity as it developed a more globose shell shape and in the long term, shells became larger. The captive population also displayed more colour polymorphism than wild caught specimens. *Partula rosea* displayed no immediate morphological differences, but long term the extant population displayed larger shell sizes compared to the wild caught specimens. Colour polymorphism can indicate high genetic diversity within the population (Murray & Clarke, 1968), therefore the captive population of *P. varia* in Sakamoto (2011) may have maintained good genetic diversity. However, the morphological changes to the shell shape (becoming more globose over time) could have negative effects on survival in the wild (Sakamoto, 2011). Wild *Partula* snail shells are more elongated, and this shape is important as it helps the snail to balance as it climbs the branches and trunks of plants and trees. The more globose shell of captive *P. varia* could potentially disrupt the centre of balance and mean that climbing vertical structures could be become difficult (Heller, 1987).

Although a management programme (EAZA Best Practice Guidelines for Polynesian tree snails, 2019) has been designed to minimise the genetic adaptation to captive conditions and to maintain known genetic lineages identified in the wild, there are still concerns about the viability of captive populations. Many of the species were founded from small numbers of wild-caught snails and have been through many generations of captive breeding. These factors raise concern about the species becoming adapted to the highly artificial captive conditions, potentially damaging their survival in natural conditions in the future (Pearce-Kelly *et al.,* 1995). Therefore, a comprehensive study comparing the morphology of wild and long-term captive bred *Partula* snail species across all the UK collections is crucial for learning about any changes that may be occurring in the morphology of the captive snails. Furthermore, if any changes are occurring in captivity that could potentially cause negative effects if the species were to be reintroduced into the wild, it is important to determine how we could alter the current husbandry guidelines to minimise any negative effects.

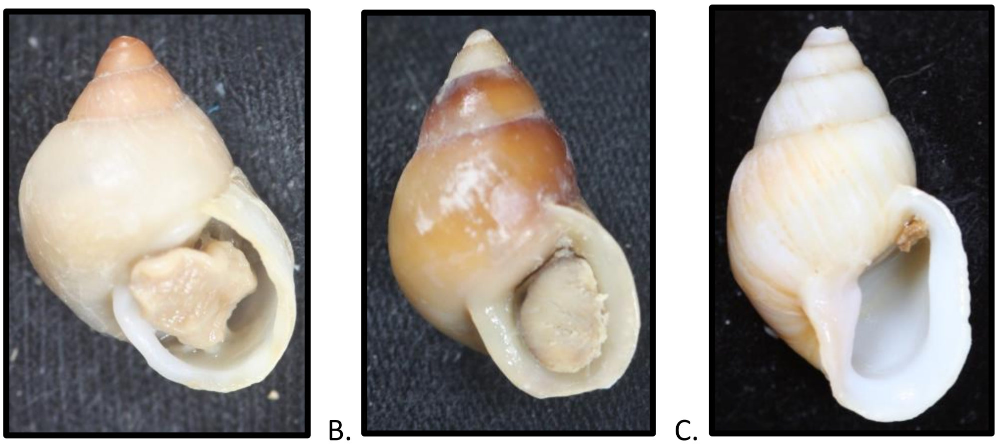
2. Methods

All specimens of 25 species of *Partula* that are preserved at ZSL London Zoo were initially incorporated in the research, including wild caught and captive bred specimens (Appendix 2). Some of the specimens were originally housed by other collections including Edinburgh Zoo, Bristol Zoo, Marwell Zoo, Chester Zoo, Jersey Zoo, Nottingham University, Thiory Zoo (France) and University of Kingston. These specimens had been sent to ZSL London Zoo for population data recording and preservation. These specimens were included in the research as these collections are part of the *Partulid* Global Species Management Programme (*P*GSMP) and each collection followed the same *Partula* husbandry guidelines, therefore the snails should not be affected by the captive bred location (P. Pearce-Kelly, personal communication, 14th March 2021). The number of species was subsequently reduced to 10 species, as only the species that had a) wild specimens, b) defined and clear captive bred generations, and c) several specimens per generation could be included to answer the study question.

Only adult snail shells were measured to provide a fair comparison between shells. To identify an adult shell there must be a visible lip that flares out from the whorl, which thickens during the reproductive stage (Clarke, 2019; Figure 3).

Figure 3. Image of an adult *P. affinis* specimen, sinistral form, showing the identifiable feature of the flared and thickened lip.

Any adult shells that were damaged or deformed were photographed for recording purposes but were not included in the geometric morphometric measurements to avoid distortion of results. Examples of shell damage appeared as chipped lips, no apex, and parts of whorls missing. Deformities included double lips or thickening of lips and areas of the shell that were damaged or dirty which meant that landmark positions could not be placed correctly (Figure 4). Advice was sought on identifying deformities from P. Pearce-Kelly and D. Clarke at ZSL London Zoo that coordinate the *P*GSMP.



A. B. C.

Figure 4. Examples of shell damage and common deformities found in the specimens: A) adult *P. hebe bella* with a double lip; B) adult *P. varia* with a chipped lip; C) adult *P. faba* with a missing apex.

2.1. Geometric morphometric analysis

Geometric morphometric analysis allows for a more in-depth analysis of the shell shape compared to morphological analyses (Crampton & Gale, 2005; Haase & Misof, 2009; Stankowski, 2011). Landmarks are placed on the image and then all landmarks are compared all other landmarks, providing greater detail of any morphological differences (Webster & Sheets, 2010), whereas traditional calliper methods can only compare one point against one other point. Every preserved adult specimen stored at ZSL London Zoo was photographed by E. Trickett using a canon E450 camera mounted onto to tripod with a 100mm macro lens facing down. Shells were placed on a mount covered in black cloth with the shell aperture facing up. A ruler was included in the image to allow for scale measurements during analysis.

Each individual specimen image was recorded by the photograph number on a Microsoft Excel spreadsheet, using this programme allowed specific searches to be conducted later in the study. A total of 10,737 specimen images were captured, 3321 of these images could not be used because the shells were deformed or damaged (Figure 4). A further 2479 specimens were removed from the data because they were crossed generations and therefore not suitable for a fair analysis. An additional 2360 specimens could not be included in the study for several reasons including lack of generations for comparison and limited data which could not be found in the timescale for the study due to national lockdowns and social distancing restrictions imposed by the UK government during 2020 during the Covid-19 pandemic. This meant that a total of 2612 specimens were included in this study from 10 species (Appendix 2).

The images were then sorted into a folder specific to the species and then by generation ready to use within the MorphoJ software v1.07a (Klingenberg, 2011). A tps file was first created for each species using tpsUtil v.1.78. The images were then randomised within the tps file and saved. The tps file was then reopened and each specimen's ID was changed to represent the species, generation, and image number according to the data collection spreadsheet. This allowed for the images to be sorted later and to easily identify the generation for each image. Landmarks were then be added to each specimen image using tpsDig232. A total number of 27 landmarks were added to each specimen image (Figure 5). Landmarks 1 to 12 were manually placed on each image, landmarks 13 to 27 were placed using the curve tool. Once all the specimens for each species had been landmarked, the data could then be used in MorphoJ. A new project was created in MorphoJ for each species and the following tasks were completed in this order for each species; outliers were found to identify any specimens that varied greatly from the majority of all the other specimens. A Procrustes Fit was conducted followed by a Wireframe where the key landmarks were connected to form an informal drawing of the shape of the shell which shows any changes in shell shape within the results (Klingenberg, 2013). A Covariance Matrix was conducted by generation followed by a Principal Component Analysis (PCA) and then finally a by Canonical Variate Analysis (CVA). The CVA was produced using 95% confidence ellipses. The CVA was chosen as it provided more detailed differentiation than the PCA to understand morphological shape change between the generations for each species.

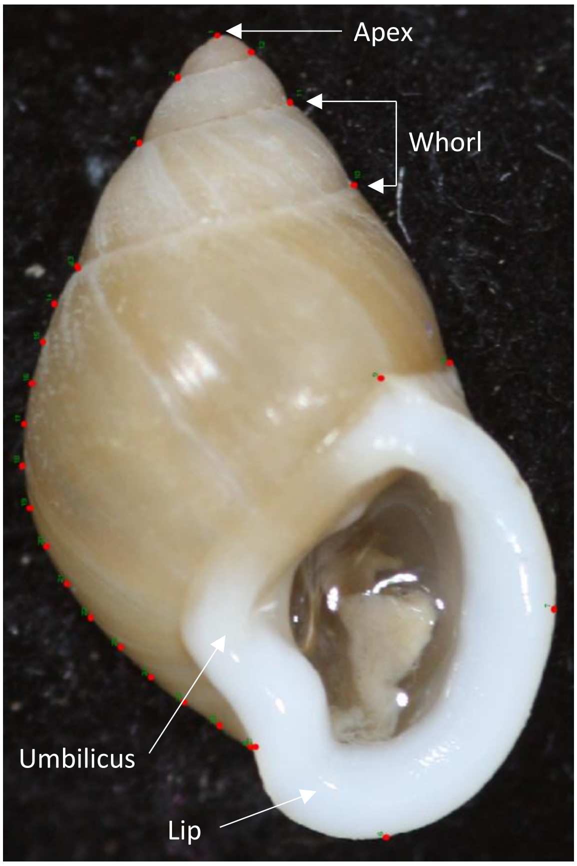


Figure 5. *Partula garretti* showcasing the position of the 27 landmarks (red dots) added in the same location to each specimen for each species, and the identifying features of the shell.

3. Results

3.1 Comparison of species with wild and long-term captive bred specimens

There were ten species of *Partula* that could be used in the research that had wild specimens that could be compared with clearly defined captive bred generations. Each species of *Partula* had different generations and varying numbers of specimens for each generation available for comparison (Table 3).

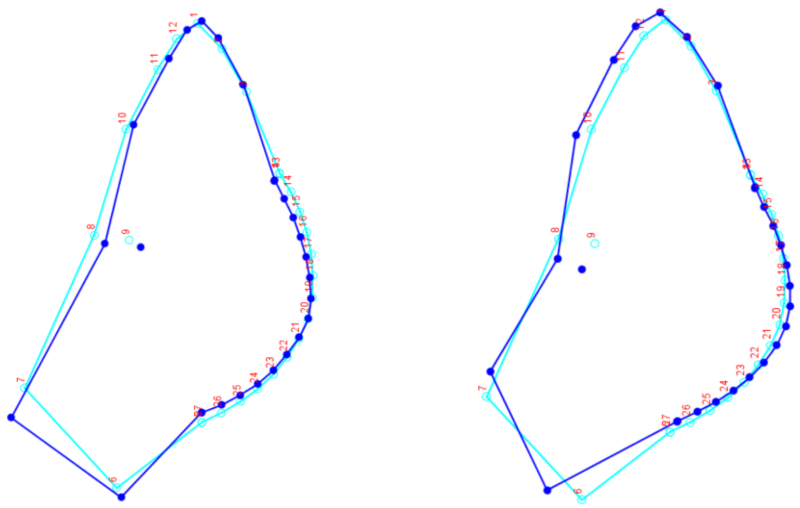
Table 3. The number of specimens available for comparison between generations for each species of *Partula* included in the research.

Species	Number of specimens included in research for each generation											
	P	F01	F02	F03	F04	F05	F06	F07	F08	F09	F10	F11
P. affinis	39	5	1		20	21	29					
P. clara	52	3		3	9							
P. faba	29	39	9	11								
P. garrettii	17	5	4	5	41	55	81	1				
P. hebe bella	3	9	6	7	1			11				
P. otaheitana	91	10	3									
P. rosea	60	1	5			2	15	2	10	15	2	
P. suturalis strigosa	2	5	27	17	32	57	38	43	17			
P. tohievana	1	17	38	25	52	73	79	91	32	4	2	4
P. varia	1088	60	52	17	8							

The first five Canonical Variate Axes (CVs) explained the majority of the shape variations for each species. However, CV1 and CV2 explained the highest percentage of shape changes and therefore are the focus for this study. Details of the first five CVs for each species can be found in Appendix 3.

3.2 Morphological cross-species comparison of wild generation

A data set was created for just the wild generation specimens of all the ten species focused on in this study. Figure 6 below shows the wireframes for CV1 and CV2 of all wild specimens for all species. CV1 accounts for 65.5% the shell's morphological variation across all the species, a slight increase in apex height, reduced shell width, reduced globosity, reduced width in the whorl section, increased lip depth and width and the point at where the lip width (landmark 7) is measured is lower. CV2 accounts for 13.8% of variations characterised by changes in apex height, width of whorl section, shell width, globosity, lip depth and the point at where the lip width is measured.



A) B)

Figure 6. Wireframes of the ten focus *Partula* species showing the morphological differences across the individual species based on their wild generations. A) CV1 wireframe, accounting for 65.5% of variation; B) CV2 wireframe, accounting for 13.8% of variation. Variation moves from the light blue line with hollow circles to the dark blue line with solid circles.

The species of *Partula* included are all significantly different to one another morphologically, except for *P. hebe bella* and *P. clara* (Table 4). These results do not include *P. suturalis strigosa* or *P. tohievana* as they had a low number of specimens available in the wild generation.

Table 4. P value results for cross-species comparison of the wild generation specimens. The non-significant different species are highlighted in a shaded cell. Excludes *P. suturalis strigosa* and *P. tohievana* as they had low wild generation representation.

***Partula* species**	*P. affinis* [39]	*P. clara* [52]	*P. faba* [29]	*P. garretti* [17]	*P. hebe bella* [3]	*P. otaheitana* [91]	*P. rosea* [60]
P. clara [52]	<.0001						

P. faba [29]	<.0001	<.0001					
P. garrettii [17]	<.0001	<.0001	<.0001				
P. hebe bella [3]	<.0001	0.0625	0.0007	0.0006			
P. otaheitana [91]	<.0001	<.0001	<.0001	<.0001	<.0001		
P. rosea [60]	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	
P. varia [1088]	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001

CVA analysis of cross-species comparison for shell morphology within the wild generation only is shown in Figure 7. A clear separation can be seen between *P. affinis* and the all the other species of *Partula* included in the research. There are clear, significant separations between all the other species, except for *P. hebe bella* and *P. clara* (Table 4). Although there is a separation between *P. hebe bella* and *P. Faba* and *P. hebe bella* and *P. garrettii,* the separation is slightly less significant than all the others (Table 4; p value 0.0007 and 0.0006 respectively).

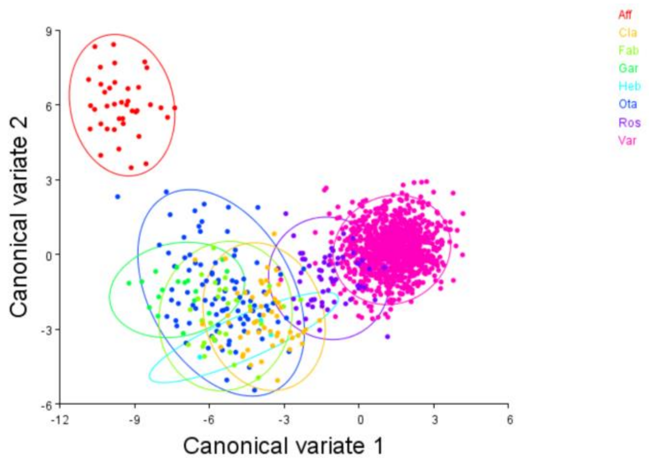


Figure 7. Comparison of CV1 and CV2 for all parent generations of all *Partula* species. Aff = *P. affinis*, Cla = *P. clara*, Fab = *P. faba*, Gar = *P. garrettii*, Heb = *P. hebe bella,* Ota = *P. otaheitana,* Ros = *P. rosea* and Var = *P. varia.*

3.3 Morphological comparison of study species; consecutive generations comparison and wild to oldest captive bred generation comparison.

CVA results of shell morphology changes between all generations of each *Partula* study species can be found in Appendix 3 The p values of generational comparison for each *Partula* study species can be found in Appendix 4. The wireframes illustrating the morphological shape changes between generations for each species can be found in Appendix 5. Table 14 provides a summary of when the morphological changes occurred within the generations for each species, along with the number of specimens included.

3.3a *Partula affinis*

Significant morphological changes appear between wild and F01 (0.0015), F04 to F05 (<.0001) and wild to F06 (<.0001). Table 5 details the significant morphological changes between these generations.

Table 5. *Partula affinis* morphological changes occurring between generations.

Generational Comparison	P value	Morphological changes	Summary of morphological changes
Wild to F01	0.0015	• Increased apex height • Widening of whorl section • Reduced lip width • Reduced lip depth	Slightly longer shells
F04 to F05	<.0001	• Reduced lip width • Reduced lip depth • Increased globosity	Narrower shells
Wild and F06	<.0001	• Reduced apex height • Increased globosity • Increased lip width	Shorter, wider, and more globose shells

3.3b *Partula clara*

Significant morphological changes appear between wild and F01 (<.0001), F03 to F04 (0.0027) and wild to F04 (<.0001). Table 6 details the significant morphological changes between these generations.

Table 6. *Partula clara* morphological changes occurring between generations.

Generational Comparison	P value	Morphological changes	Summary of morphological changes
Wild to F01	<.0001	• Reduced apex height • Increased lip depth • Increased lip width	Smaller with larger mouth
F03 to F04	0.0027	• Reduced apex height • Increased globosity	Smaller and more globose
Wild and F04	<.0001	• Increased lip width	Wider mouth

3.3c *Partula faba*

Significant morphological changes appear between wild and F01 (0.0001). Table 7 details the significant morphological changes between these generations.

Table 7. *Partula faba* morphological changes occurring between generations.

Generational Comparison	P value	Morphological changes	Summary of morphological changes
Wild to F01	0.0001	• Reduced apex height • Increased shell width • Increased lip depth • Increased lip width	Wider shell

3.3d *Partula garrettii*

Significant morphological changes appear between wild and F01 (<.0001), F05 and F06 (0.0003) and F06 and F07 (0.0087). Table 8 details the significant morphological changes between these generations.

Table 8. *Partula garrettii* morphological changes occurring between generations.

Generational Comparison	P value	Morphological changes	Summary of morphological changes
Wild to F01	<.0001	• Reduced apex height • Increased shell width • Increased lip depth • Increased lip width	Wider shell

F05 to F06	0.0003	• Reduced apex height • Increased globosity • Reduced lip depth	Smaller shell with increase globosity
F06 to F07	0.0087	• Increased apex height • Reduced globosity • Increased shell width • Increase in lip width	Longer and wider shell

3.3e *Partula hebe bella*

There are no significant morphological changes between consecutive generations for *P. hebe bella.* The only significant morphological changes detected were between wild and F04 (p = <.0001) and F02 and F07 (p = 0.0382). These changes can be seen in the CVA results for overall *P. hebe bella* morphological changes (Appendix 3). Table 9 details the significant morphological changes for CV1 and CV2.

Table 9. Significant morphological changes for *P. hebe bella* CV1 and CV2.

CVA	Variation	Morphological changes	Summary of morphological changes
CV1	38.9%	• Increased shell width • Decrease in lip depth	Shorter and narrower shell
CV2	23%	• Increased apex height • Increased whorl width • Increased shell width • Increase globosity	Longer and wider shell

3.3f *Partula otaheitana*

There are no significant morphological changes between consecutive generations for *P. otaheitana.*

3.3g *Partula rosea*

Significant morphological changes appear between F05 and F06 (0.0031), F06 and F07 (0.0161) and wild to F10 (0.0028). Table 10 details the significant morphological changes between these generations.

Table 10. *Partula rosea* morphological changes occurring between generations.

Generational Comparison	P value	Morphological changes	Summary of morphological changes
F05 to F06	0.0031	• Reduced apex height • Increased shell width • Increased globosity	Wider more globose shells
F06 to F07	0.0161	• Reduced apex height • Increased shell width • Increased lip depth	Wider shells
Wild and F10	0.0028	• Reduced apex height • Reduced lip depth	Shorter shells

3.3h *Partula suturalis strigosa*

Significant morphological changes appear between wild and F01 (0.0376) and F05 and F06 (<.0001). Table 11 details the significant morphological changes between these generations.

Table 11. *Partula suturalis strigosa* morphological changes occurring between generations.

Generational Comparison	P value	Morphological changes	Summary of morphological changes
Wild to F01	0.0376	• Increased apex height • Reduced globosity • Increased lip depth • Increased lip width	Longer and wider shells
F05 to F06	<.0001	• Increased apex height • Increased whorl width • Increased lip width	Longer and wider shells

3.3i *Partula tohievana*

Significant morphological changes appear between F01 and F02 (0.0253), F04 and F05 (<.0001), F05 and F06 (<.0001), F06 and F07 (0.0206), F07 and F08 (0.0008), F08 and F09 (0.0009), F09 and F10 (0.0537 and F10 and F11 (0.0234). Table 12 details the significant morphological changes between these generations.

Table 12. *Partula tohievana* morphological changes occurring between generations.

Generational Comparison	P value	Morphological changes	Summary of morphological changes
F01 to F02	0.0253	• Decreased apex height	Shorter shells
F04 to F05	<.0001	• Decreased apex height • Increased shell width • Increased globosity • Increased lip width	Shorter, wider, and more globose shells
F05 to F06	<.0001	• Increased apex height • Reduced globosity • Increased lip depth • Reduced lip width	Longer and narrower shells
F06 to F07	0.0206	• Increased apex height • Reduced shell width • Reduced lip depth	Narrower shells
F07 to F08	0.0008	• Reduced apex height • Increased shell width • Increased globosity • Increased lip width • Increased lip depth	Wider and more globose shells
F08 to F09	0.0009	• Increased apex height • Increased globosity • Increased lip width • Reduced lip depth	Wider and more globose shells
F09 to F10	0.0537	• Reduced apex height • Increased shell width • Increased lip width	Shorter and wider shells
F10 to F11	0.0234	• Reduced apex height • Increased globosity • Increased shell width • Increased lip width • Reduced lip depth	Shorter, wider, and more globose shells

3.3j *Partula varia*

Significant morphological changes appear between wild and F01 (<.0001) and wild and F04 (0.0001). Table 13 details the significant morphological changes between these generations.

Table 13. *Partula varia* morphological changes occurring between generations.

Generational Comparison	P value	Morphological changes	Summary of morphological changes
Wild to F01	<.0001	• Increased apex height • Reduced globosity • Reduced shell width • Increased lip depth	Longer and narrower shells
Wild and F04	0.0001	• Increased apex height • Reduced globosity • Increased lip depth	Longer and narrower shells

Table 14. Details of life history traits of each study species and highlights when the morphological changes occurred between generations for each study species. The grey boxes depict the last captive generation available for comparison. *LCG = Last Captive Generation. The figures in [ ] are the number of specimens for the respective generations mentioned. [1] Data collated by Gibbs, 1997, [2] Data collated by Gerlach 2016.

Species **Shell Shape** **Dietary** **Habitat Altitude** **Mean Shell L W A cm**	**Wild and F01**	**F01 to F02**	**F02 to F03**	**F03 to F04**	**F04 to F05**	**F05 to F06**	**F06 to F07**	**F07 to F08**	**F08 to F09**	**F09 to F10**	**F10 to F11**	**Wild to LCG***
P. affinis Conical [1] Specialist [1] All [1] 16.81 10.16 8.90 [2]	**Yes** [39, 5]	[5, 1]	[1,0]	[0,20]	**Yes** [20,21]	[21,29]						**Yes** W to F06 [39, 29]
P. clara Conical [1] Generalist [1] Mid/High [1] 15.12 8.75 8.52 [2]	**Yes** [52, 14]	[14, 0]	[0, 3]	**Yes** [3, 9]								**Yes** W to F04 [52, 9]
P. faba Globose [1] Generalist [2] All [2] 24.03 14.59 13.09 [2]	**Yes** [29, 39]	[39, 9]	[9, 11]									
P. garrettii Conical [1] Specialist [2] Low/Mid 16.27 10.30 8.96 [2]	**Yes** [17, 5]	[5, 4]	[4, 5]	[5, 41]	[41, 55]	**Yes** [55, 81]	**Yes** [81, 1]					
P. hebe bella	[3, 9]	[9, 6]	[6, 7]	[7, 1]	[1, 0]	[0, 0]	[0, 11]					

Globose [1] Specialist [2] Low/Mid [2] 15.00 10.73 8.54 [2]												
P. otaheitana Conical [1] Generalist [2] All [1] 18.50 10.55 9.56 [2]	**Yes** [91, 10]	[10, 3]										
P. rosea Conical [1] Specialist [2] All [1] 21.31 12.98 9.49 [2]	[60, 1]	[1, 5]	[5, 0]	[0, 0]	[0, 2]	**Yes** [2, 15]	**Yes** [15, 2]	[2, 10]	[10, 15]	[15, 2]		**Yes** W to F10 [60, 2]
P. suturalis strigosa Conical [1] Generalist [1] All [1] 19.04 10.55 9.75 [2]	**Yes** [2, 5]	[5, 27]	[27, 17]	[17, 32]	[32, 57]	**Yes** [57, 38]	[38, 43]	[43, 17]				
P. tohievana Globose [1] Specialist [1] Mid/High [1] 21.58 12.10 11.05 [2]	[1, 17]	**Yes** [17, 38]	[38, 25]	[25, 52]	[52, 73]	**Yes** [73, 79]	**Yes** [79, 91]	**Yes** [91, 32]	**Yes** [32, 4]	**Yes** [4, 2]	**Yes** [2, 4]	
P. varia Conical [1] Generalist [2] All [1] 17.57 10.65 9.73 [2]	**Yes** [1088, 60]	[60, 52]	[52, 17]	[17, 8]								**Yes** W to F04 [1088, 8]

4. Discussion

The first morphological comparison made was between the wild generations of each of the ten individual study species, to determine if the individual species were morphologically different. Eight species showed significant morphological differences between each species, as expected (*P. clara, P. garrettii, P. hebe bella, P. otaheitana, P. rosea, P. suturalis strigosa* and *P. varia). Partula hebe bella* and *P. clara* showed morphological similarities between the two species.

The second morphological comparisons made were based on the individual *Partula* species. This part of the study was investigating any significant morphological changes that may have occurred between the generations of the same species. The results found one species, *P. hebe bella* showed no significant morphological changes between generations, however specimen numbers available for comparison were low, thus we cannot exclude the possibility that this might be a false negative. Indeed, it is worth noting that, since each species held varying numbers of suitable specimens for each generation, there is a possibility that Type II errors could have occurred. The remaining nine species *P. affinis, P. clara, P. faba, P. garrettii, P. otaheitana, P. rosea, P. suturalis strigosa, P. tohievana and P. varia* all displayed significant morphological changes at various generational stages. Six of these species (*P. clara, P. garrettii, P. otaheitana, P. rosea, P. suturalis strigosa and P. varia)* were disregarded as the specimen counts were either to varied between the generations showing significant changes, or too low for a fair comparison/representation (Table 14). This meant that just three species (*P. affinis, P. faba and P. tohievana)* displayed fair comparative results for the purpose of this study. These three species all showed significant morphological changes in captivity at various generational stages.

This study was limited by the number of specimens available per species and per generations. The investigation was based on the largest existing collection of *Partula* shells, yet for some species or generation, not enough specimens were present to perform meaningful comparisons. This particularly applies to the results for six species

(*P. clara, P. garrettii, P. otaheitana, P. rosea, P. suturalis strigosa and P. varia)* that were removed from the analysis as the specimen numbers were considered either to varied between the generations, or too low in number for a fair comparison/representation. In other cases, small sample sizes were used (e.g., *P. hebe bella*), but the assessment of statistical power (Faul, Erdfelder, Buchner & Lang, 2009) is particularly complex when comparing multiple parameters in a multivariate analysis (Chartier & Allaire, 2007). But even if it would have been possible to detect a functionally important sample size, it would have been impossible to reach it, as all specimens that were suitable were included. Careful interpretation of the results (in particular of Type II errors), thus need to be considered.

4.1 Geometric morphometric comparison cross-species wild generation

Most of the study species were morphologically different to each other at the wild generation, which is to be expected for different species (Gerlach, 2016), although *P. hebe bella* and *P. clara* showed similarities in morphology at this generational stage. These two species are from different islands within the Society Islands. *Partula hebe bella* evolved approximately 250,000 years ago on the island of Raiatea, which appeared approximately 2.75-2.44mya and is in the west of the cluster of islands (Lee, *et al.,* 2014), and is generally a more globose shaped shell species, found from ground to mid-level habitat and is considered a specialist (Gibbs, 1997). *Partula clara* evolved approximately 500,000 years ago on the island of Tahiti, which appeared approximately 1.12-0.5mya and is in the south-east of the cluster of islands (Lee, *et al.,* 2014), and is generally a conical shaped shell, found at mid-level habitat and is considered a plant generalist. It is believed that *Partula* colonised the Society Islands through inter-island dispersal, with the founding species originating from the islands of Bora Bora or Maputi (Lee, *et al.,* 2014). However, the pattern of colonisation does not show any direct dispersal from Bora Bora or Maputi to the islands of Raiatea or Tahiti, and the distance between these two islands is nearly 150 miles with two other islands between them, Huahine and Moorea (Lee, *et al.,* 2014). Therefore, I would assume that as these species appeared at different times on different islands with no direct colonisation between the two islands of origin, there is no morphological link between the two species. It is more likely that the varying number of specimens available for *P. hebe bella* (n=3) and *P. clara* (n=52) have provided a false result, and to satisfy any morphological similarities between the two species larger sample sizes would be required, particularly for *P. hebe bella*. Then again, if specimen numbers have not been affected the results you would potentially see morphological similarities between *P. hebe bella* and other species within this study.

4.2 Morphological comparison between generations for all study species

One species displayed no significant morphological changes between consecutive generations: *P. hebe bella. Partula hebe bella* has been represented in captivity since 1991 (Clarke, 2019) with six generations suitable for comparison in this study. This species is considered to be a globose shaped shell with a specialist diet which would suggest that the species is less adaptable to changes in its environment being a k-type species (Gibbs, 1997), requiring a fairly constant and predictable environment (Reznick, Bryant & Bashey, 2002). For each generation of *P. hebe bella* included in the study there was an extremely low number of suitable specimens available for comparison (the lowest number of specimens of all the study species). Therefore, it is a strong possibility that the results for *P. hebe bella* are less reliable. To understand any morphological changes for this species a larger number of specimens would be required for all generations.

The three species that displayed significant morphological changes, *P. faba, P. affinis* and *P. tohievana* had a larger number of specimens and/or a fair number of specimens for the generation being compared. *Partula faba* displayed significant morphological changes from wild to F01 (Figure 8). The shell of *P. faba* is described as a globose-elongate shell (Gerlach, 2016) and this is one of the larger species of *Partula* growing up to 25.12cm long and 13.92cm wide (Gibbs, 1997). *Partula* are poikilothermic and therefore sensitive to environmental changes, particularly humidity and temperature

(Pearce-Kelly *et al.,* 1995 & Gouveia, 2011). It is also recognised that larger shelled species are more susceptible to desiccation (Clarke, 1997 cited in Gibbs, 1997). The temperature and humidity would have changed during the transportation period from the wild to captivity, which would have possibly led to a level of desiccation and also been a crucial change in the snail's environment. Therefore, it seems reasonable to suspect this morphological change occurred due to the change in environment. The shells morphology changed by becoming wider. *Partula faba* is a generalist species or r-type species; these species are known to be more adaptable to changes or stresses within their environment. As *P. faba* became wider in the first captive bred generation, this could be a result of species adaptation to its new environment, enabling it to increase its ability to retain more fluids (Giokas, Pall-Gergely, & Mettouris., 2014). The morphological change could also be an adaptation to increase survival through reproductive success. As we know *P. faba* is naturally a larger more globose species, and it has been proven that shell size is positively correlated with reproductive success (Barrientos, 1998; Anderson, Weaver, & Guarlnick. 2007). This species ranges all habitat altitudes, and it has been suggested that species that range all habitats also have greater reproductivity (Gibbs, 1997). Therefore, by the shells becoming wider, *P. faba* was possibly also increasing its chances of survival in the new captive environment. The results from this study show no significant morphological changes in any of the other captive generations compared, suggesting that *P. faba* did adapt to its new captive environment. However, despite the life history and ecology of this species suggesting that it should be a robust, adaptive, and successful breeder, *P. faba* did not survive in captivity. First collected from the wild in 1991 and the last known survivors were collected from Raiatea in 1992 (Gerlach, (n.d.)a), this species is likely to have suffered a genetic bottleneck (O'Regan & Kitchener, 2005). *Partula faba* did breed in captivity and produced larger than expected young, but unfortunately the last captive specimen of *P. faba* died in 2016 (D. Clarke., personal communication, 2021). The reason for its slow decline is not clear (P. Pearce-Kelly, personal communication, 2021), however it is known that a species that suffers a genetic bottleneck, which is likely for *P. faba* as small remnant populations were collected from the wild, will reproduce in captivity, but survival will be based on their abilities to adapt to their new environment. Only a proportion of those that do adapt and survive will reproduce (O'Regan and Kitchener, 2005). This supports the findings at ZSL London Zoo as they reported that the reproductive rate of *P. faba* was slow and did not sustain the survival of the species (D. Clarke, personal communication, 2021). Despite efforts to save the species from extinction, it appears even back in 1992 the survival of this *Partula* species was in jeopardy.

A) B)

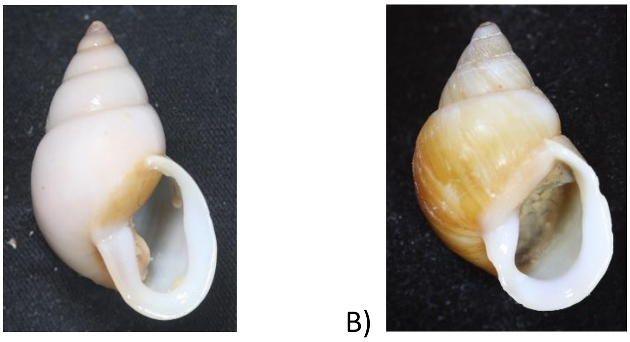


Figure 8. *Partula faba* specimens showing morphological changes between A) wild generation, described as a globose-elongate shell to B) F01 which have become wider.

Partula affinis displayed significant morphological changes between F04 [n=20] to F05 [n=21] where the shells became narrower (Figure 9). *Partula affinis* is naturally a conical shaped shell (Gibbs, 1997) and these features have been emphasised in later captivity. *Partula affinis* also displayed a significant morphological change when the wild specimens were compared with the latest captive bred generation, F06, suggesting that morphological changes have been subtly taking place throughout the captive bred populations (Figure 10). *Partula affinis* over time has become shorter, wider, and more globose. These morphological features are the opposite to the wild morphological features of the species, mentioned previously. *Partula affinis* is a specialist (k-type) species (Gibbs, 1997) and therefore does not adapt well to changes in its environment, this could be explained by the morphological changes developing subtly over the course of six captive generations. Conical shells are less likely to retain moisture (Giokas, *et al.,* 2014), and therefore by becoming wider and more globose it suggests that the greatest stress of captivity for this species was the retention of moisture to avoid desiccation. Conical shells are also known to suffer low reproductive rates and by changing the shells morphology to become wider and more globose increases the species chances of survival in captivity, which has been proven by the successful captive breeding (Gerlach., n.d.).

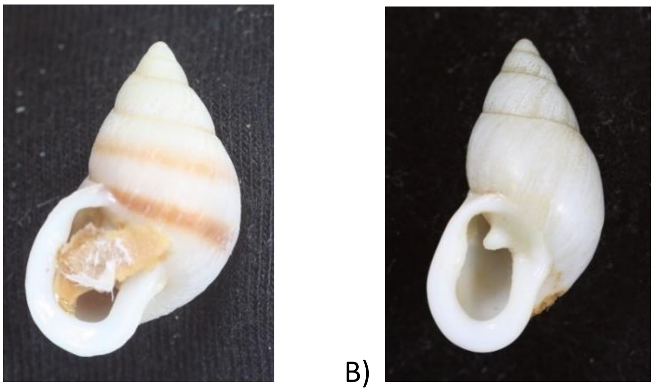
A)  B) 

Figure 9. *Partula affinis* specimens showing morphological changes between A) F04 and B) F05 which has become narrower.

A)  B) 

Figure 10. *Partula affinis* specimens showing morphological changes between A) wild generation which are naturally conical in shape and B) F06 which have become shorter, wider, and more globose in captivity.

Partula tohievana displayed significant morphological changes between F05 [n=73] to F06 [n=79] where the shells became longer and narrower (Figure 11). These morphological changes are the opposite to what this species naturally represents; a large, globose shell. *Partula tohievana* is also a specialist (k-type) species, known to be exclusively a detritivore (Gerlach, 2014) and found in the mid to high habitat altitudes (Gibbs, 1997). By becoming longer and narrower it is reducing its ability to retain moisture (Giokas, *et al.,* 2014), therefore the captive environment at this stage in its life history may have been too wet. Also, by becoming longer and narrower the species is reducing its reproductive success rate, despite this the species has shown the greatest number of captive bred generations in this study. Although other significant results were disregarded from the study for this species for reasons mentioned earlier, the species does show morphological changes occurring in several other captive generations (Table 14). It is known that local populations will display mutation events caused by gene drift when there is a limited population size (Kramarenko, *et al.,* 2020). Captive environments for *Partula* are standardised for each collection. The guidelines recommend a captive enclosure size of 50cm L x 25cm W x 30cm H with a density of up to 50 adults and their offspring, depending on the size of the snail (Clarke, 2019). It is recognised by the guidelines that immigration and emigration of the snails is needed to optimise reproductive success as the majority of *Partula* are cross-fertilising hermaphrodites (Clarke, 2019) and do not store sperm for long periods of time (Gerlach, 2016). Transferring snails to different enclosures increases the risk of infection and spread of disease to what maybe a healthy population. Currently no diseases or infections of concern appear to exist in the captive populations of *Partula* as regular screening and post-mortems take place (Clarke, 2019). *Partula tohievana* were not moved between enclosures in captivity, other than to establish a new population with juveniles and sub adults. It is also reported that *P. tohievana* did suffer a bottleneck at four individuals therefore has always experienced low genetic diversity within the captive population (D. Clarke, personal communication, 2021).



A) B)

Figure 11. *Partula tohievana* specimens showing morphological changes between A) F05 to B) F06 which has become longer and narrower.

Therefore, the underlying implication from these results appears to be that the shell morphology is specific to the species natural environment and the difference environments have the best adaptive shape (Heller, 1987; Collado, Salinas & Méndez, 2014). In captivity the environment is maintained constant (Clarke, 2009) and some species have changed morphologically from their optimal shape for the wild to a new captive shape, as the adaptive pressure has changed or modified in captivity.

4.3 Implications for conservation

Partula have suffered a rapid and extensive extinction event. Caused by the introduction of *Euglandina rosea*, populations of which are now believed to be collapsing due to unsustainable food sources and even thought to be extinct on several islands. The invasive and predatory flatworm *Platydemus manokwari* is now believed to be the greatest threat to remaining wild *Partula* species as it is present on all the islands. More recently the discovery of *Geonemertes pleaensis* another invasive predatory ribbon worm is causing concern for the survival of the species, however the extent of *G. pleaensis* is yet to be explored. (Gerlach, (n.d.)a). Sadly, captive breeding efforts were unable to save *P. faba*, however several other species remain in captivity and some have even been re-introduced into the wild and some are known to be surviving (Gerlach, (n.d.)a., Clarke, 2019).

Seven of the ten study species displayed no significant morphological changes that could be identified within this study, therefore in theory these species (*P. clara, P. garrettii, Phebe bella, P. otaheitana, P. rosea, P. suturalis strigosa* and *P. varia*) would be suitable for re-introduction. However, just because the species are suitable does not mean that the wild habitat remaining is suitable. All the study species originate from four islands in the Society islands, Tahiti, Moorea, Huahine and Raiatea. In the most recent survey of these islands' small populations of *Partula* were found, with the exception of a healthy population of *P. taeniata* on Moorea. *P. manokwari* was present on all the islands, and evidence of *E. rosea* was present on each island, often in the form of just the shell. It is even thought that *E. rosea* could be extinct on Huahine although this is not confirmed. The natural habitat has also been altered and degraded in areas, with the increase in agriculture and housing developments (Gerlach, (n.d.)a).

Three of the ten study species originate from Tahiti; *P. affinis, P. clara* and *P. otaheitana*. It is believed that a small, isolated population of *P. affinis* remains (Coote & Loeve, 2003), although no snails were found in the most recent survey of the island (Gerlach, (n.d.)a). Long-term captivity has changed the morphology of *P. affinis* and therefore casts doubt over a successful rerelease of the species. Now that the species has developed a more globose shell it has been suggested that this shape would make it more difficult for a species to climb vertical structures (Gibbs, 1997). However, *P. affinis* is a species that was found at all habitat altitudes (Gibbs, 1997) therefore may be able to survive at the lower levels with this morphological change. The habitats surveyed recently were also found to be degraded (Gerlach, (n.d.)a) which suggests that the resources required for this specialist species could be limited. The original threat to extinction, *E. rosea* appears to be declining, however the presence of *P. manokwari* is a concern, particularly as the population size is unknown. *Platydemus manokwari* is known to prey on terrestrial snails and can climb some distance vertically (Gerlach, (n.d.)a), potentially leaving *P. affinis* vulnerable to predation if it can only climb shorter vertical distances in its new morphological form. Therefore, the likelihood of a successful rerelease of *P. affinis* is a poor prospect without further investigation into the species ability to climb vertically, knowledge of *P. manokwari* population and suitability of the remaining habitat. *Partula otaheitana* and *P. clara* have been successful in captivity, developing no significant morphological changes found in this study. *Partula otaheitana* was found on the island, along with a non study species, *P. incrassa*, suggesting that the habitat is suitable for these species and to this point have managed to successfully evade predation. In the most recent survey of the island, there was no mention of any *P. clara* being found (Gerlach, (n.d.)a). I would recommend a more thorough survey of the island to search for evidence of *P. affinis, P. otaheitana* and *P. clara* to ascertain if there are any surviving populations. A population survey of *E. rosea* and *P. manokwari* and the newly identified *G. pleaensis* to understand if this invasive species is a threat to the snail populations. I also suggest a habitat survey of the area to understand what still habitat remains and whether it is suitable for these three species of *Partula*.

Two of the ten study species originate from the island of Moorea, *P. tohievana* and *P. suturalis strigosa*. A juvenile *P. tohievana* was found in the 2016 rerelease site of Belvedere in 2017 (Gerlach, (n.d.)a) suggesting that this rerelease has been successful. *Partula tohievana* was one of the species that showed a significant morphological change between F05 and F06, producing longer and narrower shells. This shape of shell is beneficial for species that prefer climbing to higher altitudes (Heller, 1987), and generally *P. tohievana* has been found at mid to high levels. Therefore, this morphological change could potentially benefit the species if it were to be rereleased. A healthy population of *P. taeniata* was found in Opunohu Bay. It is thought that *E. rosea* and *P. manokwari* would pose little threat to *P. taeniata* due to the tidal area that it was found, as the area was inhabited by crabs which were clearing any organic litter (Gerlach, (n.d.)a). *Partula taeniata* and *P. tohievana* share ecological similarities, both species are considered detritivore generalists, with *P. taeniata* found at low to mid habitat levels and *P. tohievana* found at mainly mid habitat levels, providing a clear ecological niche for each species. This information suggests that a rerelease of *P. tohievana* in Opunohu Bay could be successful. *Partula suturalis strigosa* now only exists in captivity and during this time has shown no significant morphological changes. This species is believed to have become extinct in 1987 (Coote & Loeve, 2003) due to *E. rosea* predation. In the Belverdere rerelease site only shells of *E. rosea* and one live specimen of *P. manokwari* was found (Gerlach, (n.d.)a) suggesting that the threat of predation is greatly reduced. *Partula suturalis strigosa* is a species that prefers mid-level habitats and is recognised as a generalist (Gerlach, 2016). Therefore, likely to evade any predation of *P. manokwari* if it were to be rereleased. I would recommend the following before any more species are rereleased into the area: 1) a detailed population survey of the two known predators, *E. rosea* and *P. manokwari* and a search for the newly discovered *G. pleaensis* and the threat it may pose to the snails; and 2) a survey of the habitat in Opunohu Bay to discover if this habitat would be suitable for *P. tohievana*. I believe based on this information that there is potential for a successful re-introduction of *P. tohievana* and *P. suturalis strigosa.*

Two of the ten study species originate from the island Huahine, *P. varia* and *P. rosea.* It is possible that *E. rosea* is now extinct on this island, however *P. manokwari* is abundant and no evidence of fresh *Partula* snails were found (Gerlach, (n.d.)a). During long-term captivity *P. varia* and *P. rosea* have shown no significant morphological changes and therefore would be potential species for rerelease. The habitats that were surveyed in 2017 were found to be degraded with many non-native plant species present and most of the habitat low lying (Gerlach, (n.d.)a). Both species are considered plant generalists, therefore may adapt to the change in habitat, however *P. varia* lives at all habitat levels and *P. rosea* prefers mid habitat levels (Gerlach, 2016). A change in the habitat height coupled with the fact that *P. manokwari* is abundant and can climb some distance vertically (Gerlach, (n.d.)a) may not provide a suitable rerelease habitat for these two species. I would recommend: 1) a detailed population survey of the three known predators; *E. rosea* to ascertain extinction, *P. manokwari* to understand how abundant and how it is thriving in this habitat, and a search for the newly discovered *G. pleaensis* and the threat it may pose to the snails; 2) a survey of the habitat to understand if the non-native species could be a suitable dietary resource and if they have the potential to provide the height required for the snails. A re-introduction of *P. varia* and *P. rosea* is planned (Gerlach, (n.d.)a) however I would not recommend this in the immediate future due to the abundance of *P. manokwari* and the degraded habitat that is unlikely to support the species.

Three of the ten study species originate from the island of Raiatea, *P. faba* which is now extinct in the wild and in captivity, *P. garrettii* and *P. hebe bella* which are both believed to have become extinct in the wild in 1994 (IUCN, 2021) but remain in captivity. During long-term captivity, these species have shown no significant morphological changes, and therefore have the potential for rerelease. *Partula garrettii, P. hebe bella* and a non study species *P. navigatora* were rereleased into Faaro in 2016. The rerelease was unsuccessful as the snails were predated upon by *P. manokwari* and the habitat was found to be severely degraded (Gerlach, (n.d.)a). *Partula garrettii* and *P. hebe bella* share similar ecological needs, both preferring low to mid habitat levels. *Partula garretti* is considered a generalist and *P. hebe bella* a plant generalist. Despite the habitat being severely degraded it might be expected that as generalist species they may adapt to the changed environment. It was probably the preference of lower habitat levels that contributed to their demise as *P. manokwari* are known to predate at these levels

(Gerlach, (n.d.)a). I would not recommend any further rereleases on this island due to the abundance of *P. manokwari* and the severely degraded habitat. I would recommend: 1) a detailed population survey of the three known predators; *E. rosea* to ascertain extinction, *P. manokwari* to understand how abundant and how it is thriving, and a search for the newly discovered *G. pleaensis* and the threat it may pose to the snails; 2) a survey of the habitat to discover the extent of the destruction caused by agriculture and housing developments (Gerlach, (n.d.)a) to understand if any suitable habitat remains for these species.

The risk of extinction by predation remains on all the islands, despite the reduction and even possible extinction of *E. rosea*, there appears to be a rise in the population of *P. manokwari* and a possible new threat from *G. pleaensis*. Habitat destruction is increasing, although there are areas where secondary growth is appearing, albeit predominately non-native plant species. Fragmented areas of suitable habitat are still available for some *Partula* species, knowing how inaccessible some areas of these islands are, there maybe more. Hence the need for more detailed predator and habitat survey of each island to help the breeding programme establish which species are priority in terms of potential for rerelease. Currently Tahiti and Moorea appear to be the most promising islands as possible rerelease sites for some *Partula* species and therefore strengthening relationships with local authorities and communities would benefit the species that exist and any future rerelease programmes of *Partula.*

Several specimens were excluded from the research, due to the shells displaying deformities, such as a missing apex and double lips (figure 4). These shell deformities meant that landmarks could not be placed reliably on each specimen, thus not allowing differences amongst complex shapes to be shown. The landmarks were placed on the specimens using the following criteria: 1) homologous points on the specimen, 2) adequate coverage of the morphology and 3) repeatability and reliability of marking on each specimen. The deformities described meant that these individual specimens did not satisfy these criteria and therefore had to be removed from the dataset to allow for a fair comparison. It is important to note that the use of semi-landmarks is slightly different as they are representing the curve rather than the position of the landmark, and therefore not regarded as homologous points (Zelditch, Swiderski & Sheets, 2012). Deformed shells could perhaps be included in a future study reconstructing the missing parts. Several reconstruction methods have been used in palaeoanthropology (Gunz, Mitteroecker, Neubauer, Weber, & Bookstein, 2009 & Ogihara et al., 2015), and the use of multivariate regression or thin-plate spline could be used with the support of semi-landmarks with reference to complete specimens (Deregnaucourt, Bardin, Anderson & Béthoux, 2021).

In captivity, despite the production of husbandry guidelines breeding can become difficult to manage as the number of generations increases and space to house individual generations is limited, thus generations were not often kept separated. Several cross-generational specimens were removed from the dataset. This study just focused on the specimens that were from defined generations to allow for a clear comparison between generations. Nevertheless, there is potential for a further study to compare also the cross-generational specimens for geometric morphometric differences.

This study has only investigated the external morphology of the species and how this may be affected by captivity. The internal morphology of captive animals can also be affected by the diet that they are provided. A nutritious and easily digestible captive diet can have a significant effect on gut morphology which could have a negative effect on the survival of any rereleased captive-bred animals, where diets will be poorer and less easy to digest (O'Regan & Kitchener, 2005). This internal morphological change has been studied in birds and found that shorter intestines and caeca, lighter hearts, livers, and gizzards were developed compared to wild birds. This meant the captive-bred birds were less able to digest their natural food and handle any toxins that the foods may contain (Liukkonen-Anttila, Saartoala & Hissa, 2000). Captive *Partula* are provided with a nutritious and easily digestible diet, it would be beneficial to study any possible changes of the internal morphology of the species using data collected (Gerlach, 2016) and from preserved captive specimens.

4.4 Captivity recommendations

The work that the collections have done to date to provide *Partula* with an environment that allows the species to survive, and breed has been successful nearly all of the species in captivity. Only three species in this study have shown any significant morphological change whilst in long-term captivity, one of these is now extinct, *P. faba* and nothing further can be done for this species. The one lesson that can be learnt from this loss is not to assume that because a species is considered to be robust and adaptable to changes in its environment that it will adapt and change. *Partula tohievana* and *P. affinis,* despite changing morphologically during their time in long-term captivity, still have the potential for rerelease in the future, and although *Partula* maybe poikilothermic (Pearce-Kelly *et al.,* 1995; Gouveia, 2011), they are also demonstrating plasticity in response to their environment and predators (Trussell, 2000) which means that if rereleased they could once again change their morphology to suit their environment and aid their survival. *Partula tohievana* may even have increased its chances of survival in the wild with the new morphological changes.

5. Conclusion

A comprehensive study of ten *Partula* species has been completed comparing the morphology of wild and long-term captive bred snails. The study found that the morphology of three species had altered during captivity. One of these species, *P. faba,* is now extinct and nothing further can be done for this species. *Partula affinis* appears to have been changing subtly throughout captivity and overall has become shorter, wider, and more globose. These changes are likely to have been a gradual adaptation to its captive environment allowing the species to survive in captivity. The captive morphology differs to the wild morphology; however, it is still possible that this species could be reintroduced knowing that its wild counterparts have survived at all habitat levels. If captive bred specimens were to be rereleased, it would struggle to climb vertical heights due to the shells more globose shape, however the species would have the potential to survive at the lower habitat levels. There is uncertainty to the existence of *P. affinis* in the wild. Further studies into the morphological changes of *P. affinis* could be conducted, based on the morphological changes found and the possible reasoning for these changes. The captive bred specimens in this study have become wider and more globose, suggesting that the species adapted to retain more moisture in captivity. Environmental data from wild habitats could be collected and compared with captive environmental data to ascertain if the reason for this morphological change is correct. *Partula tohievana* only showed a significant morphological change between F05 and F06, becoming longer and narrower, opposite features to the wild specimens. This could possibly be a mutation event due to limited captive population size and low genetic diversity within the captive population. This species could follow a similar route as *P. faba* and possibly become extinct in captivity over time due the low genetic diversity. This species does exist in the wild from a successful rerelease from captive specimens. The remaining seven species did not show any significant morphological changes in captivity, *P. clara, P. garrettii, P. hebe bella, P. otaheitana, P. rosea, P. suturalis strigosa* and *P. varia,* suggesting that the current husbandry guidelines are suitable for captive care of this species. All these species therefore have the potential to be rereleased into habitat suiting their environmental needs. However, the underlying theme for the survival of all *Partula* species in the wild is the threat of predators. The threat from *E. rosea* has reduced but not disappeared, there is an increased threat from *P. manokwari* as the population has grown and appears to more widespread, and a newly discovered invasive species *G. pleaensis* is unknown potential threat to the species. Habitat destruction and fragmentation of habitat also seems to be an increased risk to the species survival, caused by the increased human population and the need to convert land for agricultural purposes. Therefore, although some of these species have been saved from extinction through the creation of the captive breeding programme, there is still uncertainty as to whether or not their wild environment remains suitable for them to thrive once more.

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7. Appendix

7.1 Appendix 1. Colour morph detail found in literature and recorded for *Partula* species.

Species	**Colour/banding detail**	**Reference**
Partula affinis	Several colour morphs recorded, including banding.	Crampton, 1916
Partula nodosa	4 colour classes, including banded and unbanded.	Crampton, 1916
Partula radiolata	6 colour morphs and patterns.	Crampton, 1925
Partula gibba	At least 7 colour morphs.	Crampton, 1925
Partula tohiveana	3 colour morphs.	Crampton, 1932
Partula mooreana	2 colour morphs.	Crampton, 1932
Partula suturalis strigosa and *Partula suturalis vexillum*	Colour variation varies from valley to valley location.	Crampton, 1932
Partula taeniata	7 colour morphs.	Crampton, 1932
Partula faba	Varying colour morphs.	Garrett, 1884
Partula varia	High degree of colour variation, virtually no two snails are the same.	Garrett, 1884
Partula hyalina	White shell, no colour variation	Crampton, 1916
Partula clara	Striking colour variation, 3 colour classes created for ease of research: lighter, darker and banded.	Crampton, 1916
Partula otaheitana	4 colour classes, including banded and unbanded.	Crampton, 1916
Partula atilis	1 colour	Crampton, 1956
Partula leptochila	3 colours	Crampton, 1956
Partula cuneata	1 colour	Crampton, 1956
Partula levistraiata	1 colour	Crampton, 1956
Partula cedista	1 colour	Crampton, 1956
Partula garretti	1 colour	Garrett, 1884
Partula turgida	1 colour	Garrett, 1884
Partula rosea	7 colour morphs	Garrett, 1884

Partula dentifera	2 colour morphs	Garrett, 1884
Partula lugubris	1 colour	Garrett, 1884

7.2 Appendix 2. All 25 *Partula* species that were data recorded by generation. The table shows the generations preserved for each species √ and the 10 species of Partula that were the focus of the research as they help wild specimens for comparison with defined captive bred specimens identified by *.

Species	Generation	Included in Research	Reason for not being included in research
P. affinis *	F01	√	
	F02	√	
	F04	√	
	F05	√	
	F06	√	
	Wild	√	
	XGEN		Mixed generation
P. clara *	F01	√	
	F03	√	
	F04	√	
	Wild	√	
	XGEN		Mixed generation
P. faba *	F01	√	
	F02	√	
	F03	√	
	F03-04		Mixed generation
	F04-05		Mixed generation
	Wild	√	
P. garrettii *	F01	√	
	F02	√	
	F03	√	
	F04	√	
	F05	√	
	F05-06		Mixed generation
	F06	√	
	F07	√	
	Wild	√	
P. gibba	F02	√	
	F03	√	
	F04	√	
	F05	√	
	F06	√	
	F07	√	
	F08	√	
	F09	√	
	F10	√	

	F11	√	
	XGEN		Mixed generation
P. hebe bella *	F01	√	
	F02	√	
	F03	√	
	F04	√	
	F07	√	
	Wild	√	
	XGEN		Mixed generation
P. hyalina	F01-02		Mixed generation
	F02		Only 1 generation, nothing to compare
	XGEN		Mixed generation
P. labrusca	F01-02		Mixed generation
	F02-03		Mixed generation
	P-01		Mixed generation
	XGEN		Mixed generation
P. lirata	Wild		Too few specimens for viable comparison
	F01		Too few specimens for viable comparison
P. lutea	Wild		Only 1 generation, nothing to compare
P. mirabilis	F03	√	
	F04	√	
	F06	√	
	F06-07		Mixed generation
	F07	√	
	F08	√	
	F09	√	
	XGEN		Mixed generation
P. mooreana	F01	√	
	F01-02		Mixed generation
	F01-04		Mixed generation
	F02	√	
	F02-03		Mixed generation
	F02-05		Mixed generation
	F03	√	
	F03-04		Mixed generation
	F03-06		Mixed generation
	F04-05		Mixed generation
	F04-07		Mixed generation
	F05-06		Mixed generation
	F06	√	
	F06-07		Mixed generation

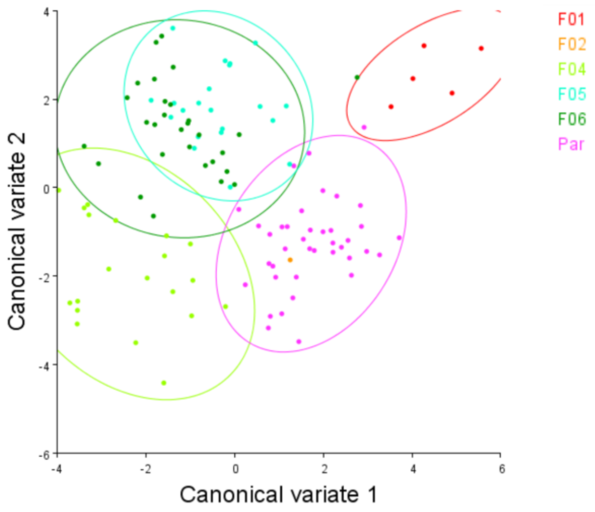
	F07	√	
	F07-08		Mixed generation
	F08	√	
	F08-09		Mixed generation
	F09	√	
	F09-10		Mixed generation
	F10	√	
	F11	√	
	F12-13		Mixed generation
	XGEN		Mixed generation
P. navigatoria	F01-02		Mixed generation
	F02-03		Mixed generation
	F03-04		Mixed generation
	F04-06		Mixed generation
	F05-06		Mixed generation
	F06-07		Mixed generation
	P-01		Mixed generation
	Wild		Only 1 generation, nothing to compare
	XGEN		Mixed generation
P. nodosa	XGEN		Mixed generation
P. otaheitana *	F01	√	
	F01-02		Mixed generation
	F02	√	
	F02-03		Mixed generation
	Wild	√	
	XGEN		Mixed generation
P. radiolata	F02	√	
	F03	√	
	F04	√	
	F05	√	
	F06	√	
	F07	√	
	XGEN		Mixed generation
P. rosea *	F01	√	
	F01-02		Mixed generation
	F02	√	
	F05	√	
	F06	√	
	F07	√	
	F08	√	
	F09	√	
	F10	√	
	F11-12		Mixed generation
	Wild	√	

	XGEN		Mixed generation
*P. suturalis strigosa **	F01	√	
	F01-02		Mixed generation
	F01-03		Mixed generation
	F02	√	
	F02-03		Mixed generation
	F02-04		Mixed generation
	F03	√	
	F03-04		Mixed generation
	F03-05		Mixed generation
	F04	√	
	F05	√	
	F05-06		Mixed generation
	F06	√	
	F06-07		Mixed generation
	F07	√	
	F08	√	
	Wild	√	
	XGEN		Mixed generation
P. suturalis vexillum	F01	√	
	F01-02		Mixed generation
	F01-03		Mixed generation
	F02	√	
	F02-04		Mixed generation
	F03	√	
	F03-04		Mixed generation
	F03-05		Mixed generation
	F04	√	
	F04-05		Mixed generation
	F05	√	
	F07	√	
	F10	√	
	F11	√	
	X01		Mixed generation
	X03		Mixed generation
	XGEN		Mixed generation
P. taeniata elongata	XGEN		Mixed generation
P. taeniata nucleola	XGEN		Mixed generation
P. taeniata simulans	F06	√	
	F07	√	
	F08	√	
	F09	√	
*P. tohievana **	F01	√	

	F02	√	
	F03	√	
	F04	√	
	F05	√	
	F06	√	
	F06-07		Mixed generation
	F07	√	
	F08	√	
	F09	√	
	F10	√	
	F11	√	
	Wild	√	
	XGEN		Mixed generation
P. turgida	F01	√	
	F02	√	
	F03	√	
	Wild	√	
*P. varia **	F01	√	
	F01-02		Mixed generation
	F02	√	
	F03	√	
	F04	√	
	Wild	√	
	XGEN		Mixed generation

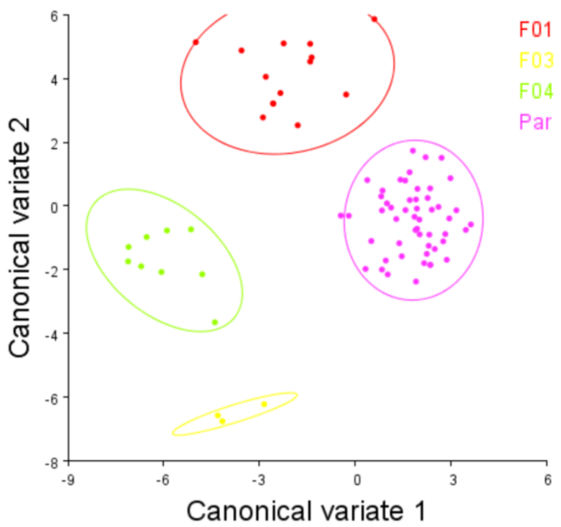
7.3 Appendix 3. CVA results of shell morphology changes between all generations of each *Partula* study species.

<u>*Partula affinis*</u>



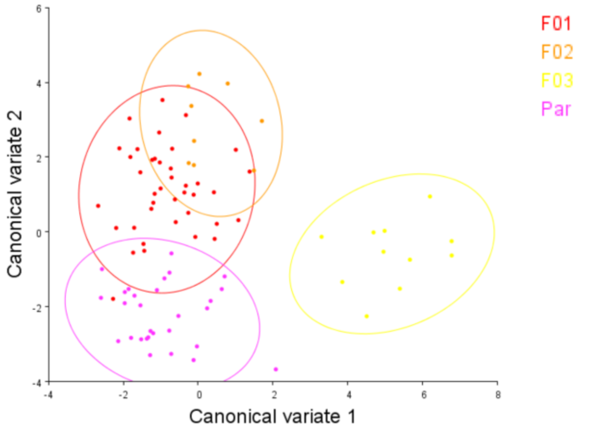
Partula affinis		
CV	Eigenvalues	% Variance
1	0.00069031	35.648
2	0.00044670	23.068
3	0.00022283	11.507
4	0.00015063	7.779
5	0.00008774	4.531

<u>*Partula clara*</u>



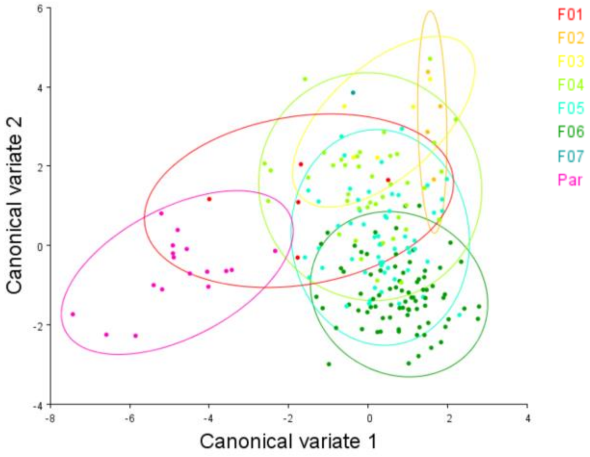
Partula clara		
CV	Eigenvalues	% Variance
1	0.00155024	54.328
2	0.00041343	14.488
3	0.00025465	8.924
4	0.00017078	5.985
5	0.00012350	4.328

Partula faba



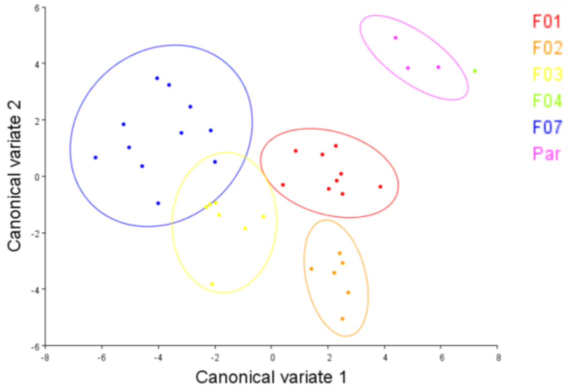
Partula faba		
CV	Eigenvalues	% Variance
1	0.00067075	31.942
2	0.00039188	18.662
3	0.00028810	13.720
4	0.00021461	10.220
5	0.00016710	7.958

Partula garrettii



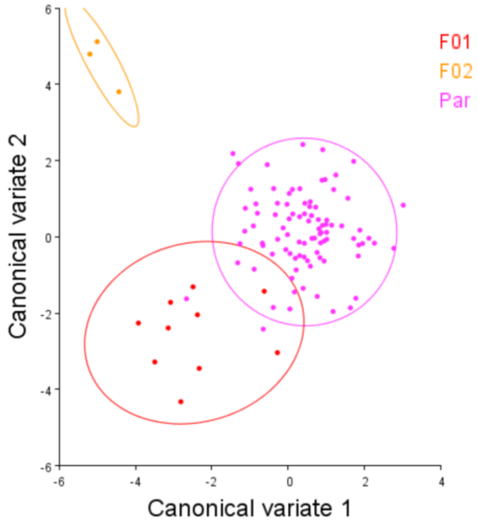
Partula garretti		
CV	Eigenvalues	% Variance
1	0.00066955	41.054
2	0.00025778	15.806
3	0.00017691	10.847
4	0.00013217	8.104
5	0.00009935	6.092

Partula hebe bella



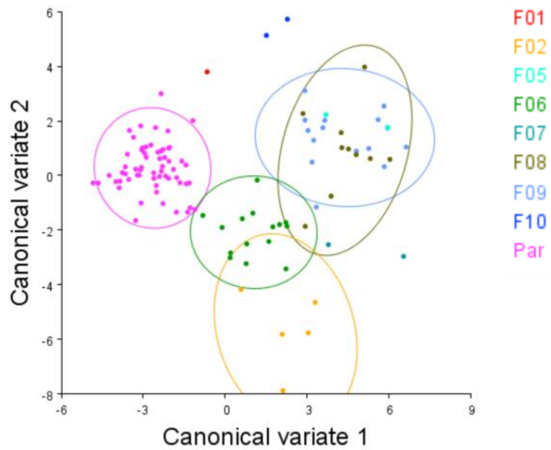
Partula hebe bella		
CV	Eigenvalues	% Variance
1	0.00068664	38.878
2	0.00040651	23.017
3	0.00022832	12.928
4	0.00011647	6.594
5	0.00010164	5.755

Partula otaheitana



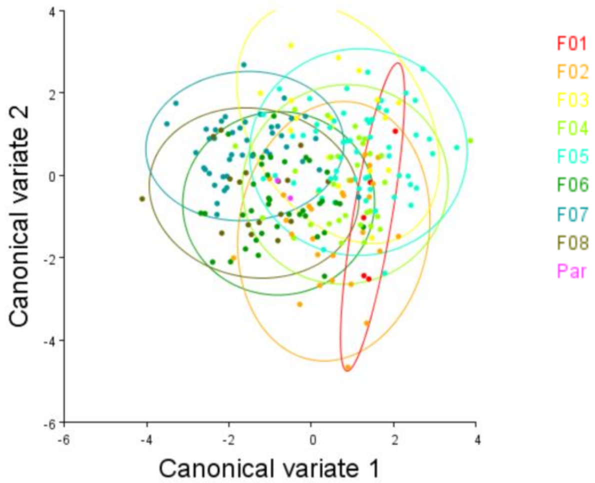
Partula otaheitana		
CV	**Eigenvalues**	**% Variance**
1	0.00111129	39.492
2	0.00049983	17.762
3	0.00044416	15.784
4	0.00020000	7.107
5	0.00016883	6.000

Partula rosea



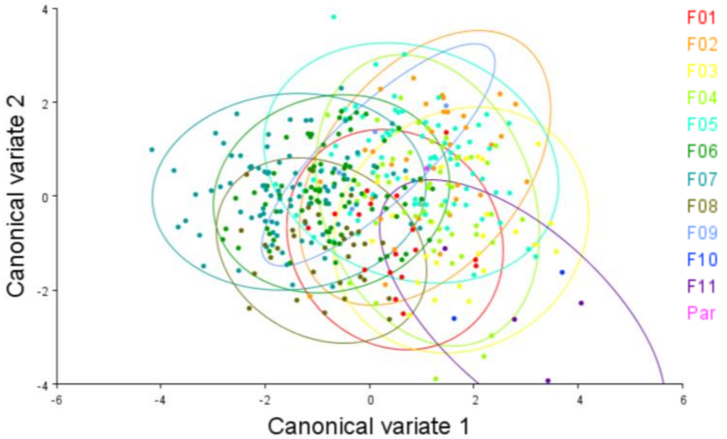
Partula rosea		
CV	**Eigenvalues**	**% Variance**
1	0.00043431	32.509
2	0.00022281	16.677
3	0.00017376	13.007
4	0.00016350	12.238
5	0.00008305	6.217

Partula suturalis strigosa



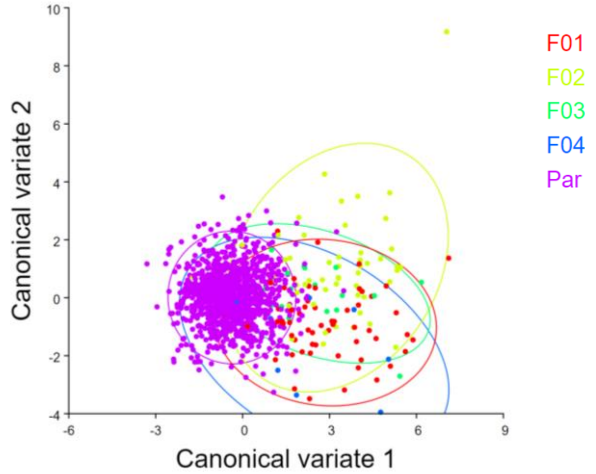
Partula suturalis strigosa		
CV	**Eigenvalues**	**% Variance**
1	0.00067549	33.131
2	0.00041659	20.432
3	0.00025651	12.581
4	0.00017396	8.532
5	0.00009368	4.595

Partula tohievana



Partula tohievana		
CV	**Eigenvalues**	**% Variance**
1	0.00058112	26.126
2	0.00052409	23.562
3	0.00032496	14.610
4	0.00021964	9.875
5	0.00017034	7.658

Partula varia



Partula varia		
CV	**Eigenvalues**	**% Variance**
1	0.00056591	34.776
2	0.00029375	18.052
3	0.00022915	14.082
4	0.00013300	8.173
5	0.00011235	6.904

7.4 Appendix 4. Generational comparison of the 10 *Partula* study species. The number of specimens per generation are in brackets next to the generation. Shaded cells represent significant values and the values in bold are the values of interest for comparison between consecutive generations and comparison between wild specimens and oldest captive bred generation.

Partula affinis							
	Par [39]	F01 [5]	F02 [1]	F03 [0]	F04 [20]	F05 [21]	F06 [29]
Par [39]	–	**0.0015**	0.1030		<.0001	<.0001	**<.0001**
F01 [5]		–	0.8632		0.0010	0.0209	0.0048
F02 [1]			–		0.7017	0.6813	0.6696
F03				–			
F04 [20]					–	**<.0001**	<.0001
F05 [21]						–	0.0649
F06 [29]							–

Partula clara					
	Par [52]	F01 [14]	F02 [0]	F03 [3]	F04 [9]
Par [52]	–	**<.0001**		0.0001	**<.0001**
F01 [14]				0.0010	<.0001
F02 [0]			–		
F03 [3]				–	0.0027
F04 [9]					–

Partula faba				
	Par [29]	F01 [39]	F02 [9]	F03 [11]
Par [29]	–	**0.0001**	0.1242	0.0756
F01 [39]		–	0.8094	0.0122
F02 [9]			–	0.1167
F03 [11]				–

Partula garretti								
	Par [17]	F01 [5]	F02 [4]	F03 [5]	F04 [41]	F05 [55]	F06 [81]	F07 [1]
Par [17]	–	**<.0001**	<.0001	0.0001	<.0001	<.0001	<.0001	0.0508
F01 [5]		–	0.3884	0.8484	0.5555	0.2169	0.0019	0.1531
F02 [4]			–	0.7310	0.2998	0.0470	0.0001	0.6324
F03 [5]				–	0.7373	0.0652	0.0003	0.2831
F04 [41]					–	0.0028	<.0001	0.0326
F05 [55]						–	**0.0003**	0.0464
F06 [81]							–	**0.0087**
F07 [1]								–

Partula hebe bella								
	Par [3]	F01 [9]	F02 [6]	F03 [7]	F04 [1]	F05	F06	F07 [11]
Par [3]	–	0.3513	0.0915	0.1631	<.0001			0.2323
F01 [9]		–	0.3119	0.5627	0.0783			0.1590
F02 [6]			–	0.3941	0.2408			0.0382
F03 [7]				–	0.0631			0.1188
F04 [1]					–			0.0836
F05						–		
F06							–	
F07 [11]								–

Partula otaheitana			
Par [91]	Par [91]	F01 [10]	F02 [3]
F01 [10]	–	0.0004	0.1191
F02 [3]		–	0.1356
			–

Partula rosea										
	Par [60]	F01 [1]	F02 [5]	F03	F04	F05 [2]	F06 [15]	F07 [2]	F08 [10]	F09 [15]	F10 [2]
Par [60]	–	0.6877	<.0001			0.0002	<.0001	0.0007	<.0001	<.0001	**0.0028**
F01 [1]		–	0.3306			0.3278	0.0571	0.3335	0.1734	0.0975	0.3307
F02 [5]			–			0.1654	0.0001	0.3205	0.0026	<.0001	0.3208
F03				–							
F04					–						
F05 [2]						–	**0.0031**	0.6650	0.0097	0.1005	0.3365
F06 [15]							–	**0.0161**	0.0134	<.0001	0.0616
F07 [2]								–	0.5573	0.6780	0.6687
F08 [10]									–	0.6827	0.4090
F09 [15]										–	0.3734
F10 [2]											–

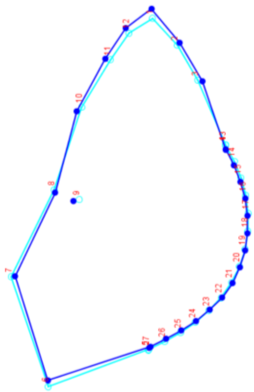
Partula suturalis strigosa									
	Par [2]	F01 [5]	F02 [27]	F03 [17]	F04 [32]	F05 [57]	F06 [38]	F07 [43]	F08 [17]
Par [2]	–	**0.0376**	0.0928	0.2128	0.1659	0.2338	0.5520	0.2925	0.3686
F01 [5]		–	0.6940	0.1461	0.5198	0.4824	0.0064	0.0042	0.0291
F02 [27]			–	0.0853	0.7521	0.1200	0.0001	<.0001	0.0224
F03 [17]				–	0.4068	0.3230	0.0060	0.0010	0.0797
F04 [32]					–	0.4858	0.0002	<.0001	0.0466
F05 [57]						–	**<.0001**	<.0001	0.0091
F06 [38]							–	0.5445	0.6481
F07 [43]								–	0.6879
F08 [17]									–

Partula tohievana												
	Par [1]	F01 [17]	F02 [38]	F03 [25]	F04 [52]	F05 [73]	F06 [79]	F07 [91]	F08 [32]	F09 [4]	F10 [2]	F11 [4]
Par [1]	–	0.6024	0.5905	0.9416	0.7806	0.7445	0.6894	0.3889	0.2231	0.0838	0.6700	0.0999
F01 [17]		–	**0.0253**	0.0966	0.0177	0.0001	0.0408	0.0003	0.0236	0.0217	0.0419	0.0007
F02 [38]			–	0.1146	0.0104	0.0315	0.0075	<.0001	0.0003	0.2294	0.1405	<.0001
F03 [25]				–	0.2778	0.0179	0.0034	0.0001	0.0001	0.2512	0.4038	0.0056
F04 [52]					–	**<.0001**	<.0001	<.0001	<.0001	0.4068	0.1529	<.0001
F05 [73]						–	**<.0001**	<.0001	<.0001	0.4379	0.1573	<.0001
F06 [79]							–	**0.0206**	0.005	0.1369	0.0939	0.0003
F07 [91]								–	**0.0008**	0.0668	0.0310	<.0001
F08 [32]									–	**0.0009**	0.0005	<.0001
F09 [4]										–	**0.0537**	0.0264
F10 [2]												**0.0234**
F11 [4]												–

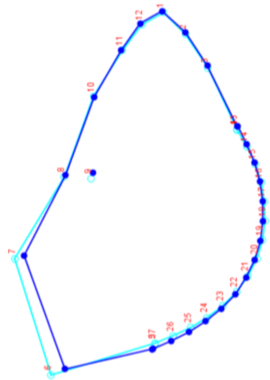
Partula varia					
	Par [1088]	F01 [60]	F02 [52]	F03 [17]	F04 [8]
Par [1088]	–	**<.0001**	<.0001	<.0001	**0.0001**
F01 [60]		–	0.3500	0.2380	0.1713
F02 [52]			–	0.5460	0.2420
F03 [17]				–	0.5843
F04 [8]					–

7.5. Appendix 5. Wireframes of each significant generational comparison for all *Partula* study species.

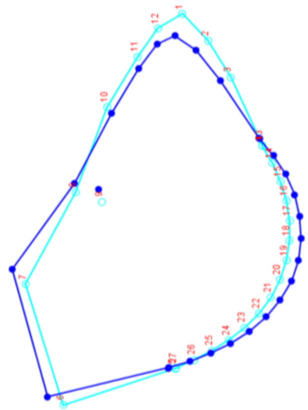
<u>*Partula affinis*</u>



Wild to F01

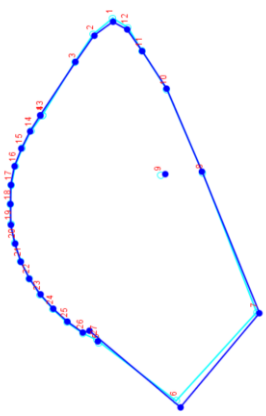


F04 to F05

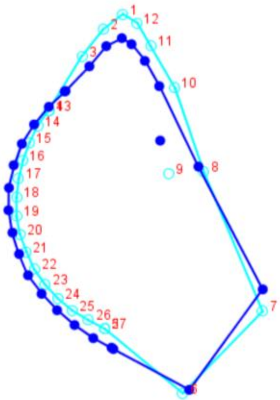


Wild to F06

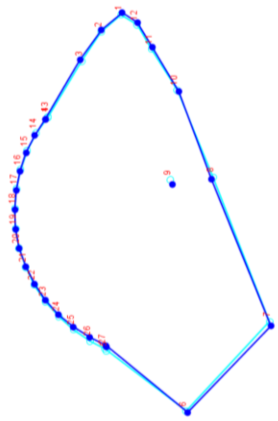
<u>*Partula clara*</u>



Wild to F01

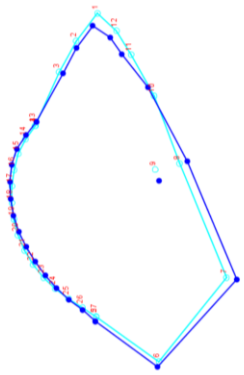


F03 to F04



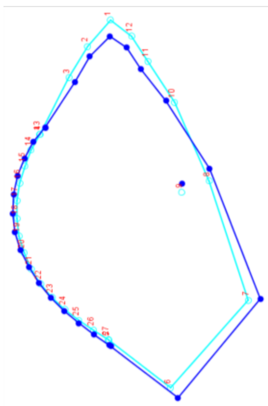
Wild to F04

Partula faba

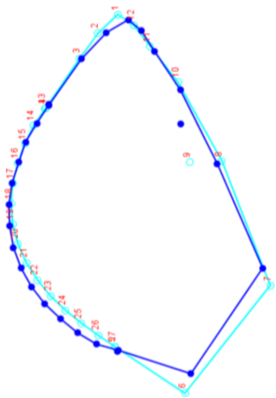


Wild to F01

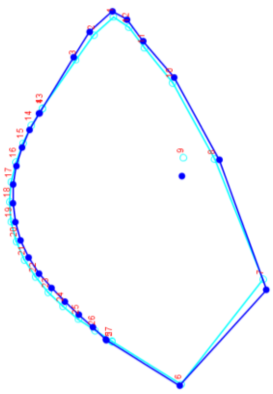
Partula garrettii



Wild to F01

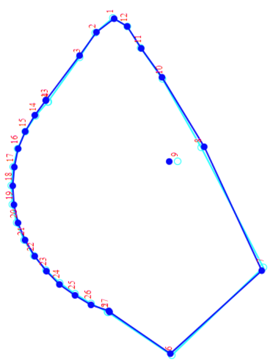


F05 to F06

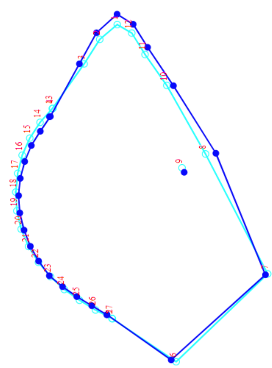


F06 to F07

Partula hebe bella

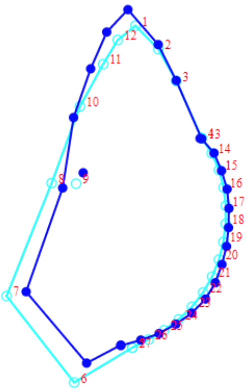


CV1

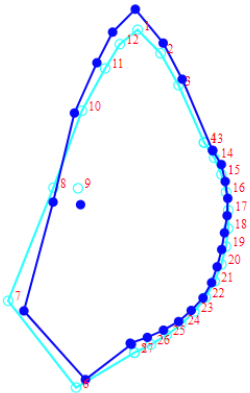


CV2

Partula otaheitana

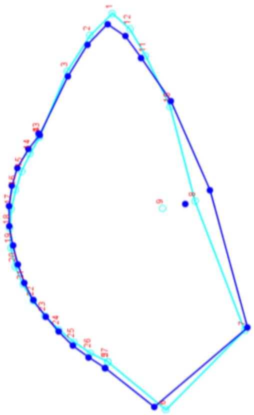


CV1

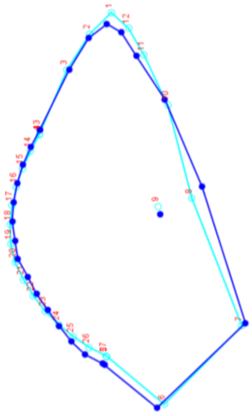


CV2

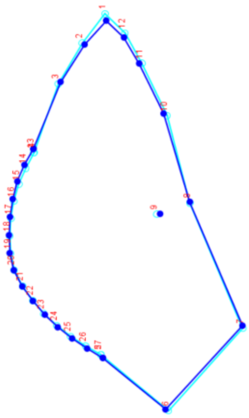
Partula rosea



F05 to F06

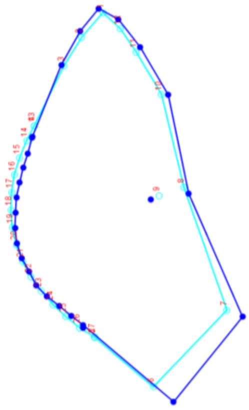


F06 to F07

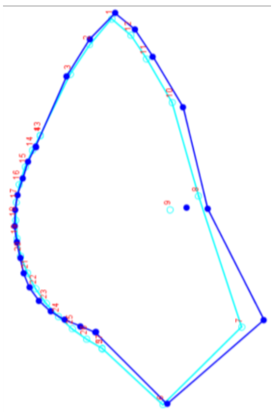


Wild to F10

Partula suturalis strigosa

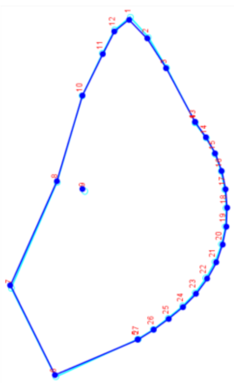


Wild to F01

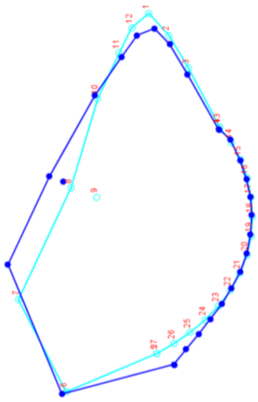


F05 to F06

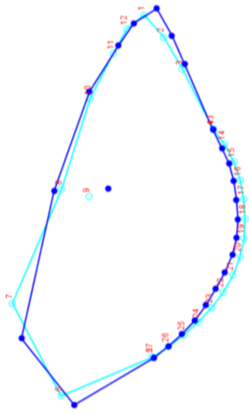
Partula tohievana



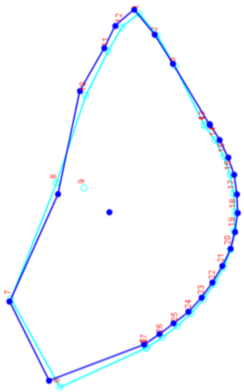
F01 to F02



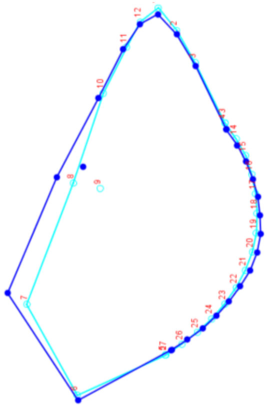
F04 to F05



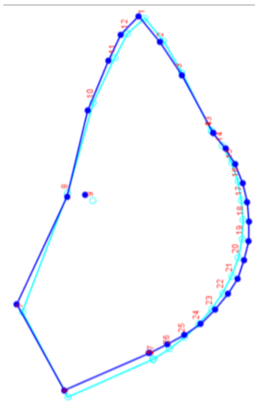
F05 to F06



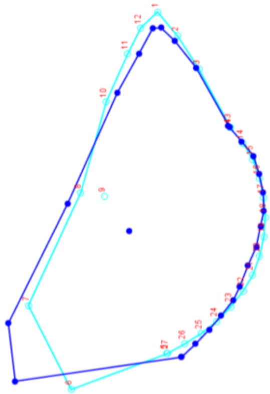
F06 to F07



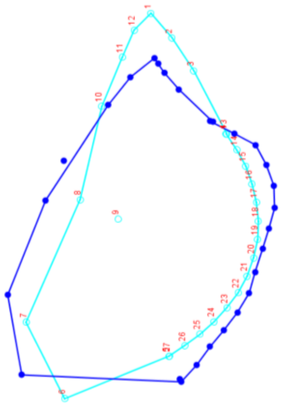
F07 to F08



F08 to F09

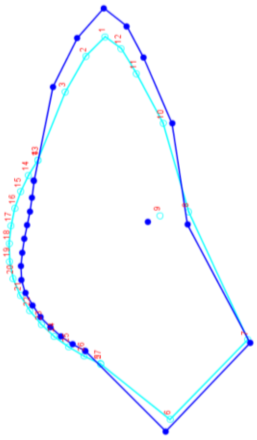


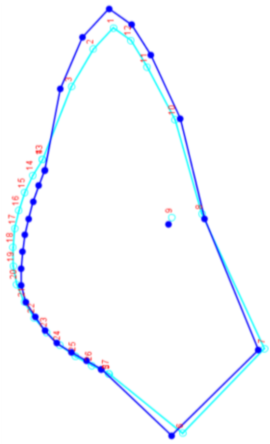
F09 to F10



F10 to F11

Partula varia


Wild to F01


Wild to F04