Sinistral Coiling in the Arboreal Snail *Partula gibba* Férussac, 1821 (Stylommatophora: Partulidae) from Guam, Mariana Islands

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RESEARCH NOTE

Sinistral coiling in the arboreal snail *Partula gibba* Férussac, 1821 (Stylommatophora: Partulidae) from Guam, Mariana Islands

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Abstract: Based on museum specimens and zooarchaeological material recovered by us, we note the historic presence of a population of sinistrally coiling *Partula gibba* Férussac, 1821 on the island of Guam. A single extinct population of this species is also known on an island > 150 km to the north. Hence, given the absence of sinistral populations on intervening islands and lack of indigenous cultural transport, we suggest that sinistrality independently evolved at least twice in *P. gibba*, the only species of *Partula* Férussac, 1821 outside of Polynesia to regularly display reverse coiling.

Keywords: Micronesia, enantiomorphy, chirality

Among gastropods, the direction of shell coiling is essentially a fixed feature of most species. Enantiomeric forms, *i.e.*, individuals displaying a coiling reverse that of most conspecifics, while known in many species, remain exceedingly rare. This pattern of occurrence is consistent with several hypotheses for the rarity of sinistrality, for example, that shell coiling is a heritable character under positive frequency-dependent selection (Davison, Barton *et al.* 2009, Grande and Patel 2009, Hoso *et al.* 2010, Shimizu *et al.* 2013). Conversely, intermediate-frequency, mixed (enantiomorphic) coiling is reported from only a very few species of gastropods. Largely unexplained is that nearly all of them are tropical, insular and arboreal land snails in the genera *Achatinella* Swainson, 1828 (Achatinellidae), *Amphidromus* Albers, 1850 (Camaenidae), *Liguus* Montfort, 1810 (Bulimulidae), and *Partula* Férussac, 1821 (Partulidae) (Laidlaw and Solem 1961).

Partula, is widely distributed across the western Pacific Ocean, with about 100 described species, all endemic to a single or a few adjacent islands (Cowie 1992). Most species are dextral but a few species, all from the Society or Samoan Islands in Polynesia, are strictly sinistral (Pilsbry 1909–1910, Crampton 1932). Additionally, several other species, also from these islands, exhibit low levels of enantiomorphy (Pilsbry 1909–1910). In these species, coiling direction opposite that of the parent can occur in a single brood regardless of the parental coiling direction (Crampton 1932, Davison, Barton *et al.* 2009).

By contrast, all of the approximately 42 other species of *Partula* were thought to be strictly dextral until Haltenorth and Jaeckel (1941 in Kondo 1970) discovered an enantiomorphic population of *P. gibba* Férussac, 1821, endemic to the Mariana Islands in Micronesia. These snails were restricted to the central highlands of one island, Saipan. Subsequently, in 15 collections (n = 14 to 222 specimens) from the area taken between 1949 and 1952, Kondo (1970) and colleagues found that about 2–35% of the snails in each collection, and nearly 12% over the entire area (n = 1736), were sinistral. Other populations on Saipan are apparently entirely dextral (Crampton 1925). A re-survey of the area *circa* 1990 led Smith and Hopper (1994) to conclude that the enantiomorphic population on Saipan, including those sampled by Kondo, had vanished. Today, only at most several small and isolated populations of *P. gibba* remain on Saipan, all of them apparently dextrally coiling (Hadfield 2015, A.M. Gawel, pers. comm., AMK, pers. obs.).

In this note, we report on the historic occurrence of at least one population of enantiomorphic *Partula gibba* from another of the Mariana islands, Guam, 218 km south-west of Saipan (Fig. 1). Most of these specimens are from collections made in the late 19th century by the French naturalist and explorer Antoine-Alfred Marche. We also report and figure another sinistral example of *P. gibba* from Guam collected by us in 2013.

Partula gibba is one of the most widely distributed species of *Partula* and has been reported from most of the more southern islands of the Mariana archipelago (Fig. 1): Aguiguan, Alamagan, Anatahan, Guam, Pagan, Rota, Saipan,

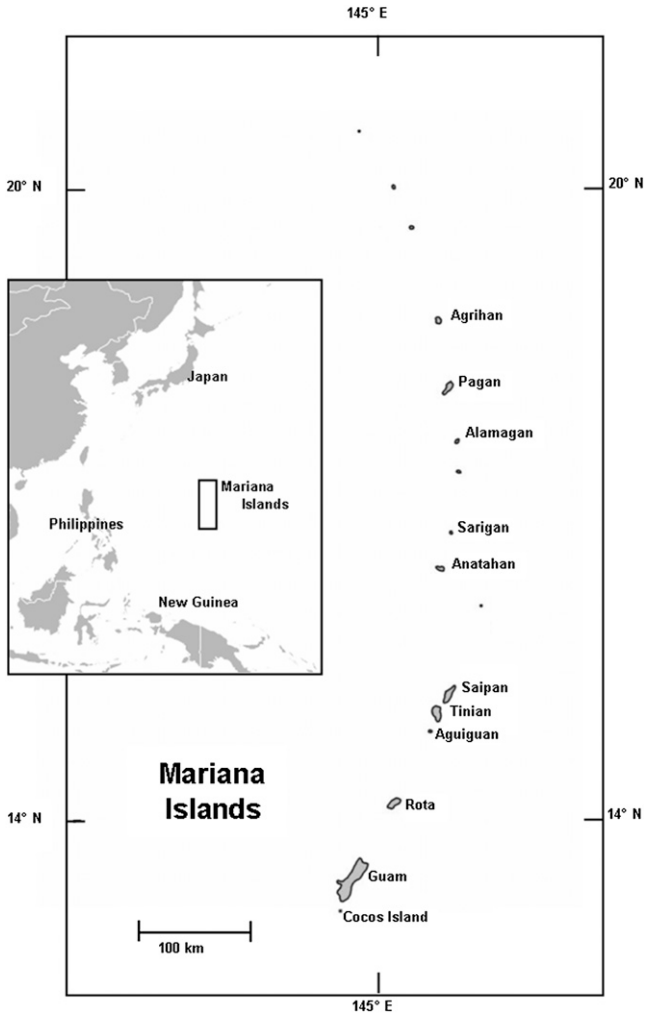

Figure 1. Map of the Mariana Islands, Micronesia (after Bauman 1996), identifying islands mentioned in the text.

Sarigan, and Tinian (Kondo 1970, Kurozumi 1994). The species' abundance was drastically reduced during the late 20th century on most islands. Most declines have been due to introduction of generalist predators (Hopper and Smith 1992). The gastropods in the genus *Gonaxis* Taylor, 1877 (Streptaxidae) and *Euglandina rosea* (Férussac, 1821) (Spiraxidae) were intentionally introduced to control another invasive species, the giant African snail *Lissachatina fulica* (Bowdich, 1822) (Achatinidae) (see Mead 1961), but appear to have gone extinct in the Marianas (Hopper and Smith 1992). The current main predator, a bipaliid flatworm *Platydemus manokwari* Beauchamp, 1962, was probably inadvertently imported in soil accompanying ornamental plants (Sugiura and Yamaura 2009, Smith 2013). As a result, *P. gibba* has probably been eliminated from Aguiguan (Smith 2013) and endures as one or two small populations on Guam, Pagan, Rota, Saipan, Sarigan, and Tinian (Hadfield 2015). Its persistence, and in some cases, even its historical occurrence, on other islands is uncertain. For example, intense and sustained volcanism since 2003 has probably buried all populations of this species on Anatahan (see Kessler 2011).

Most of the sinistral specimens of *Partula gibba* that we report and figure below are from the collections of Antoine-Alfred Marche. He visited the Mariana Islands from April 1887 to May 1889 to examine the natural history of the archipelago at the behest of the Muséum national d'Histoire naturelle (MNHN) in Paris (Marche 1891, Cheng 1982). While in the Marianas, he visited six of the archipelago's 14 main (> 5 km^2) islands, spending most of his time exploring the largest, most populated and southernmost island of Guam, but also exploring as far as the currently uninhabited and volcanically active islands of Agrihan and Pagan (Fig. 1). His report mentions marine, freshwater and land snails. Upon his return to France in July 1889, he deposited his Mariana collections, including his snails, at the MNHN, where they currently reside.

We examined all specimens of partulids collected from the Mariana Islands and held at the MNHN. Two unnumbered MNHN lots of mostly *Partula gibba* shells probably belong to Marche's Mariana collection. In the first lot of 152 shells, an old hand-written label (Fig. 2a), gives Marche as the collector, Guam as the collecting locality, and a collection date of 1888. This lot contains 146 shells of *P. gibba*, as well as two shells of the Guam endemic *P. radiolata* (Pfeiffer, 1846), plus four non-partulid shells. Among the *P. gibba* there are 127 shells of adults (having an apertural lip) to subadults (having at least four whorls, but lacking a lip) and 19 shells of embryos, provisionally also of this species. Four or 3.1% of the non-embryonic *P. gibba* shells in this lot are of sinistral forms (Fig. 2b).

The second lot has only a recent label on which is handwritten "[Guam?]" and, hence, in this paper we additionally consider this lot separately from the undoubted Marche lot described above. Still, we provisionally refer it to his collection for the following reasons: 1) it is the only other large MNHN lot of *Partula gibba*; 2) the diversity of color forms is similar to those in the labelled lot, including the preponderance of the geographically more restricted "unicolor" forms *sensu* Crampton (1925); 3) some of the shells are similarly lightly soiled with a fine black residue concentrated suturally; 4) they are of a similar lustre and wear, and hence apparent age, as the first lot; and 5) it is the only other lot that also includes a small proportion of sinistral examples. This second lot is of 93 shells of adult to subadult *P. gibba*, of which three (3.2%) are sinistral adults (Fig. 2c).

In the combined lots, then, seven (3.2%) of the subadult to adult *Partula gibba* shells ($n = 220$) are sinistral. No other collectors (Crampton 1925, Y. Kondo, unpubl., Hopper and

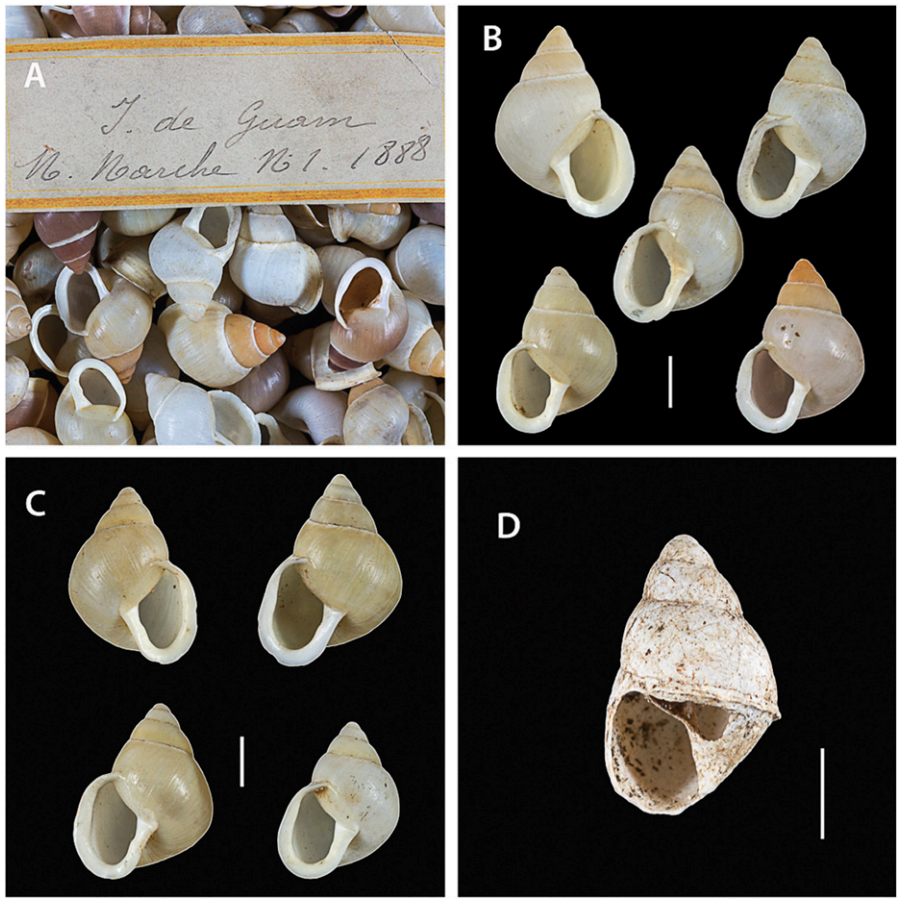

Figure 2. Sinistrally coiling *Partula gibba* Férussac, 1821 from Guam, Mariana Islands. **A,** Undoubted lot (NMHN unnumbered) of A. Marche's specimens, showing early label. **B,** Sinistral specimens and a co-collected dextral example from Marche's undoubted lot. **C,** Sinistral specimens with a co-collected dextral example from the lot putatively collected by Marche. **D,** Single sinistral partial shell discovered in 2013 in northern Guam (BPBM 278616). Scale bars: B, C, D = 5 mm. (Color shown in electronic version only).

Smith 1992, Hadfield 2015, S. Bauman, pers. comm., J. Starmer, pers. comm., AMK, pers. obs.), despite the many thousands of shells taken on Guam, have reported even a single sinistral exemplar of *P. gibba*. This argues that Marche's sinistral snails were probably collected from a single or perhaps a few clustered localities, and have not been sampled on Guam before or since. The only known remaining colony of *P. gibba* on Guam consists of a few hundred individuals and is entirely dextral (GCF, pers. obs.). Hence, Marche's enantiomorphic population on Guam is almost certainly now extinct.

Chirality in *Partula* and in other species can be associated with differences in shell size and proportions between the chiral morphs (Gould *et al.* 1985, Johnson 1987, Davison, Constant *et al.* 2009). To investigate this possibility in *P. gibba*, we compared measurements taken with Vernier calipers of the sinistral shells ($n = 7$) to an equal sized random sample of dextral shells paired with the two MNHN lots. Definitions of shell characters and measurements follow Perez and Cordeiro (2008). First, we found no significant differences in average size using one-way ANOVAs at a type I error rate $\alpha = 0.05$ between Marche's undoubted and suspected lots when holding coiling direction and measurement type constant ($df = 1,5$; $F \leq 6.53$; $p \geq 0.051$). Hence, in subsequent tests, we combined lots within coiling direction and shell dimensions. Nevertheless, we were unable to detect significant differences between sinistral and dextral samples in shell height, shell width, aperture height or aperture width (Table 1).

Marche (1891) does not record in his travelogue the precise locality or localities within Guam from which he obtained his specimens of *Partula gibba*. Unlike in Polynesia, partulids were not used in indigenous culture and have not been recovered from archaeological horizons in the Marianas, hence human transport from Saipan to Guam (or vice versa) is unlikely. Of the many sites on the large (544 km^2) island then hosting the ubiquitous species (Quoy and Gaimard 1833, Crampton 1925), we can suggest only a likely general

Table 1. Comparison of shell dimensions of *Partula gibba* from Marche's lots from Guam. Measurements in millimeters are expressed as a sample mean (and one sample standard deviation). n = sample size. One-way ANOVAs compared shells of sinistral *P. gibba* to those of dextral conspecifics, where p is the right-tail probability of an F distribution with degrees of freedom $df = 1,12$ as defined by the sample statistic F_s.

Coiling	Shell height	Shell width	Aperture height	Aperture width	n
Sinistral	16.87 (1.05)	12.60 (0.85)	9.89 (0.63)	7.47 (0.62)	7
Dextral	17.16 (0.96)	12.06 (0.65)	10.29 (0.48)	7.14 (0.18)	7
F_s	0.28	1.78	1.79	1.83	
p	0.61	0.21	0.21	0.20	

location for Marche's collection(s). Based on Crampton's (1925) extensive analysis of color variation in *P. gibba*, many of the Marche's shells can be assigned to a color form ("unicolor") seen by Crampton (1925) only in northern and central Guam. Further, six of Marche's seven sinistral shells are of this color form. We have surveyed the remaining extant populations on Guam and have seen only dextral individuals. We have also searched numerous areas in northern and central Guam for old *P. gibba* shells from leaf litter and have collected or seen several hundred dextral specimens.

However, among these shells we found a single sinistral specimen (Fig. 2d) from *Vitex*-dominated secondary forest on the northern plateau of Guam above Tarague (13.589°N, 144.901°E), and now deposited at the Bernice P. Bishop Museum (BPBM 278616). Further, this locality is also only one of two sites on Guam recorded by Crampton (1925) as definitively hosting the dominant color form displayed by Marche's sinistral shells. The shell was found in a deep crevice under a limestone boulder in association with shells of dextrally coiling *P. gibba*, as well as shells of other species of land snails. It is damaged and missing its body whorl, is bleached and very eroded (Fig. 2d), as were many of the other associated shells, including those of an introduced molluscivorous species, *Euglandina rosea*. If these other shells are contemporaneous, then the death of the sinistral specimen can be bracketed after *E. rosea*'s date of introduction ca. 1958 (Mead 1961), but before the latter species' extirpation pre-1990 (Hopper and Smith 1992). Alternatively, the shells are from a mixed time horizon and the sinistral specimen could be much older (*sensu* Bauman and Kerr 2013).

Species of molluscs with stable low-level enantiomorphy are extremely rare, occurring most commonly in a few genera of terrestrial snails (Laidlaw and Solem 1961). Why, how, and how often enantiomorphic species arise and persist are unsettled questions (Schilthuizen and Davison 2005, Hoso *et al.* 2010). Multiple instances of the evolution of enantiomorphy within a species has been less often considered, but provides insight into the relative importance of origination versus selection in the maintenance of enantiomeric forms. For example, parallel evolution of enantiomorphic populations has conceivably occurred in the European aquatic snail *Lymnaea stagnalis* (Linnaeus, 1758) (Lymnaeidae). Low-level enantiomorphy in this species has been recorded historically at several sites in the southern United Kingdom (Schilthuizen and Davison 2005). However, this species is capable of wide dispersal by humans and even by several species of waterfowl (van Leeuwen and van der Velde 2012), the populations may have been established by dispersal from a single source. In this note, we report the possible parallel and independent acquisition of enantiomorphy by a Guam population of *Partula gibba*, a species previously only known to have exhibited reverse coiling on the island of Saipan, approximately 150 km to the north (Kondo 1970).

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"**Note added in proof:** As of November 1, 2015, all extant partulid species from the Mariana islands (*Partula gibba, P. radiolata*, and *Samoana fragilis*) have been designated as endangered species, and are now protected under the U.S. Endangered Species Act. Threats to native terrestrial gastropods in the region include introduced predators, such as the flatworm *Platydemus manokwari*, and habitat degradation by human development and introduced ungulates. Studies on the basic biology and life histories of these tree snails will be important for future conservation efforts."