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ENVIRONMENTAL STRESS AND ITERATIVE PAEDOMORPHISM IN SHELLS OF *POECILOZONITES* (GASTROPODA: GASTRODONTIDAE) FROM BERMUDA

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ABSTRACT: **Considerable refinement of the surficial geology and biostratigraphy Bermuda has resulted in the proper ordering of the phylogenetic sequence of *Poecilozonites*, and thus offers an opportunity to examine evolutionary pathways within this taxon. Paedomorphism, the retention of juvenile ontogenetic characteristics into adulthood, is a recurrent morphological manifestation in fossil land snail shells of the subgenus *P.* (*Poecilozonites*) on this isolated oceanic island. The paleontology of this endemic taxon has been examined over the past century and was a key example of "punctuated equilibria" (PE) in the late 1960s and early 1970s. In a previous study, we documented the biostratigraphy and geochronology from the known fossil record of *P.* (*Poecilozonites*) representing *at least* the past 500 kyr. Here we focus specifically on paedomorphic forms that appeared in shells at the onset of the last interglaciation, marine isotopes stages (MIS) 6/5e and again at the beginning of the Holocene (MIS 2/1). There are many possible mechanisms to explain the occurrence of paedomorphism including PE, but of importance to this discussion is that neither the size nor the fossil record of *Poecilozonites* show three independent lineages as proposed by Gould (1969). Gould's several named paedomorphic forms supposedly branching from *P. bermudensis* over the past 300 kyr, occur only during the last interglacial (*sensu lato*) MIS 5, and the Holocene (MIS 1). Both punctuation and stasis characterize the morphological changes of this taxon over the past 140 ka, but these changes are reversible, and no speciation is evident.**

INTRODUCTION

The geology and paleontology of Bermuda have been of scientific interest for over a century (e.g., Gulick 1904; Pilsbry 1924; Sayles 1931; Bretz 1960). Fossil land snails of the endemic subgenus *P.* (*Poecilozonites*) (Gastrodontidae) exhibit a wide variety of shell morphologies throughout the latter half of the Quaternary of the North Atlantic island of Bermuda, located 1000 km ESE of Cape Hatteras, North Carolina (Fig. 1). Because of its important role in evolutionary theory, *Poecilozonites* is among the most intensely studied and snail populations on a remote oceanic island.

The many variants of *Poecilozonites* were originally split into distinct species or subspecies and came to be regarded as a remarkable example of "an adaptive radiation comparable in scope with the classic insular speciation and ecologic differentiation of Darwin's finches and Hawaiian honeycreepers" (Gould 1968, p. 83; 1969). Subsequent to Gould's landmark observations, a revised physical stratigraphy and geochronology of both surface deposits (Vacher et al. 1989, 1995; Hearty et al. 1992; Hearty 2002), and those in caves and fissure fills (Hearty et al. 2004), led to dramatically different concepts on the evolution of the island as well as this taxon. In a comprehensive study incorporating most of the known collections on Bermuda from at least the middle Pleistocene, it was established that *P.* (*Poecilozonites*) constitutes a single anagenetic series (Hearty and Olson 2010). The significance of the previous binomial or trinomial nomenclature established by Gould is no longer clearly verified; thus, we employ the uppercase abbreviations of the main morphotypes (Table 1; Fig. 2) explained in, and adapted from Hearty and Olson (2010).

Among our collections, shell size (height + width) varies from about 15 mm to over 65 mm (Appendix 1). Gigantism arose repeatedly within this lineage after each colonization by large vertebrate predators during glacial lowstands when the Bermuda platform was fully exposed (Olson et al. 2005; Olson and Hearty, 2010). In contrast, the onset of interglacial sea-level highstands reduced land area, introduced new environmental challenges, drove the extinction of predators, and lessened the pressure on terrestrial creatures.

The iterative evolution of paedomorphs in *Poecilozonites* became one of the main examples in the fossil record used to epitomize the hotly debated theory of PE in the origin of species (Eldredge and Gould 1972; Gould 1977, p. 276, fig. 47; see also Brown 1987). However, the physical fossil data from the Bermuda example of PE fostered by Gould has not been critically examined from a biostratigraphic perspective since their work in the early 1970s.

Paedomorphic forms of *Poecilozonites* are characterized by lower, flatter shells, with a more sharply defined (carinate) outer margin that appeared to be "scaled up replicas of juvenile shells" of "the central stock *P. bermudensis zonatus*" (Gould 1968, p. 81). According to Gould (1968, 1969), while *P. cupula* and *P. nelsoni* species flourished independently on the island, paedomorph forms branched from the non-paedomorphic *P. b. zonatus* on at least four different occasions over more than 300 ka. Gould (1970) further postulated that the supposedly thinner shell of paeodmorphs was a response to limited calcium supply on the red soils of glacial periods. We have previously established, however, there has never been any shortage of calcium for shell-building on the limestone-capped island of Bermuda. With the exception of the major deep-red soil separating the early and middle Pleistocene (our "Big Red Soil" or BRS), glacial age soils generally contain minimally 60% and generally over 90% $CaCO_3$ in the habitable soil layers for *Poecilozonites* (Ruhe et al. 1961; Olson and Hearty 2007), as well as in food plants adsorbing minerals from the ubiquitous limestone substrate through their roots.

We fully accept Gould's original proposition that paedomorphosis is the likely explanation for the shell shapes in the morphs in question and also

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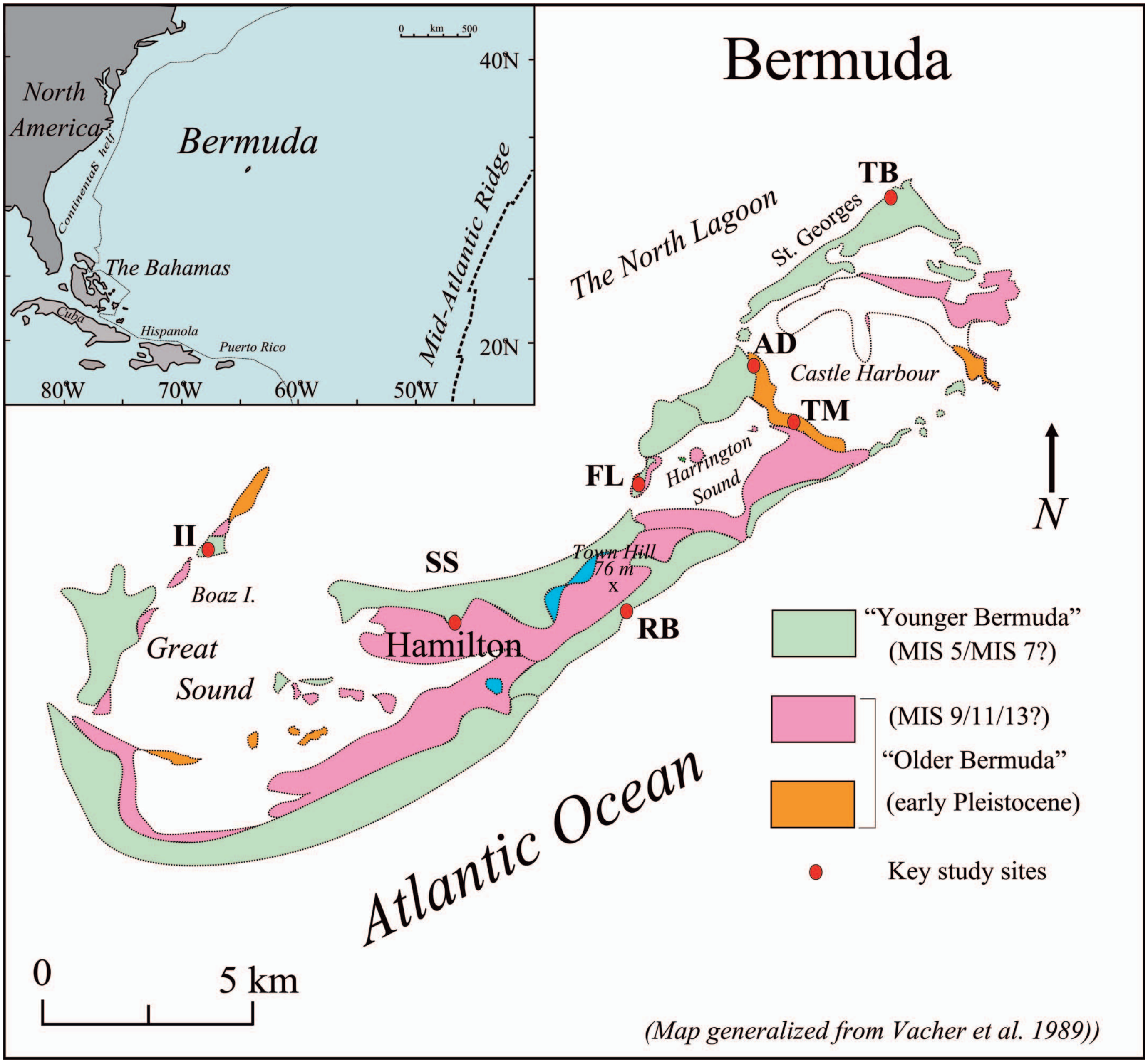

FIG. 1.—The Bermuda Islands in the North Atlantic Ocean. The Bermuda platform covers about ~ 650 km^2 while a generalized geologic map of the present Bermuda Islands covers ~ 56 km^2. Early and middle Pleistocene of "Older Bermuda" (Sayles 1931) landscapes are highlighted in gold and pink (after Vacher et al. 1989). These higher areas may have offered refuge to land snails and other invertebrates during flooding events during later interglacial highstands. "Younger Bermuda" is colored in light green. Key sites (site #) are as follows (Table 2): II = Ireland Island (#12; SJG10); SS = Saltus School (#46); RB = Rocky Bay (#33); FL = Flatts Bus Stop (#51); TB = Tobacco Bay (#25); TM = Tom Moore's Caves (#6); and AD = Admiral's Cave (#1). Further data are available in Online Supplemental Files (Tables S1, S2; Fig. S2A–S2C), and previous works (e.g., Gould 1969 (appendices and figures therein); Olson et al. 2005; Hearty and Olson 2010).

that those shapes evolved independently several times over glacial-interglacial cycles. Our revised bio-chronostratigraphy, however, imposes very different sequences of shell forms and explanations for these phenomena. The best-documented example in the fossil record of the origin of a paedomorph in the subgenus *Poecilozonites* involves the Holocene and modern endpoint *P. b. bermudensis*.

The stratigraphic and geochronologic data associated with the known populations of paedomorphs and associated shell forms that occurred since Termination II, or the MIS 6/5e transition (~ 135–130 ka) are presented here. We then examine the hypothesis that each of these paedomorphic populations evolved independently from the preceding giant, glacial age form of *P.* "*nelsoni*" (NEL6) that was the manifestation of this lineage that existed in the previous glacial period (MIS 6). Similarly, NEL4 exclusively dominated land snail fossil deposits during the glacials (MIS 4-2) (Hearty et al., 2004) and gave rise to *P. b. bermudensis* (BERM) around the time of Termination I (MIS 2/1) and Holocene. Finally, our results are reviewed in light of their historical significance of *Poecilozonites* on the hypothesis of PE.

TABLE 1.—*Correlation table of nomenclature associated with the stratigraphy of Bermuda. Units in Admirals Cave and Wilkinson Quarry are correlated with marine isotope stages (MIS); MIS events in column 5 correspond with events in Figure 6. Range of A/I (ratio of D-alloisoleucine/L-isoleucine) on Poecilozonites for each morphotype are indicated in column 4. See Figure 2 for identification of fossil elements in column 4.*

(Gould 1969, p. 414)	Hearty (2002) [sedimentary facies]	Hearty et al. (2004): "pitfalls" and Admiral's Cave	Hearty and Olson 2010 Morphotype [mean A/I]	(MIS) correlation
Recent (R)	Recent [surface live; cave deposits]	Unit y/z and Grand Canyon Cave; Tom Moore's Cave	FASO BERM [0.014–0.22]	1
		Unit w/x	NEL4	2/1
	St. Georges Soil [cave deposits and fissures]	Unit v and Wilkinson Q Rail fissure	[0.23–0.49]	3
		Unit uv		4
Southampton (S)	Southampton Fm. [eolianite and multiple protosols]	Unit u Wilkinson Q High fissure		5a
St. George's (SG) Spencer's Point Pembroke (P)	New name: Hungry Bay Fm. (HB) [eolianite and protosol]		ZONA + PAED2 [0.36–0.45]	5c
Harrington (H)	Harrington soil [weak reddened paleosol]		[Weak soil]	5e/5c
Devonshire (D)	Devonshire marine—Rocky Bay Formation (RBF) (max. +6-9 m), including Spencer's Pt. [forshore, eolianite, multiple protosols] RBF	Unit s/t	SIMU SIGL ZONA +	Late 5e
	Mid-5e regression; red colluvium	Unit r/s	PAED1	Middle 5e
	New name: Grape Bay Mb of RBF	Unit p/q/r	[0.45–0.66	Early 5e
Shore Hills (SH)	Red geosol (?) [complex paleosol]	Unit o/~p Crane fauna	NEL6 [0.60–0.74]	Late 6 to early 5e
Belmont (B)	Harvey Rd Q. [eolianite]			7/9?

METHODS AND MATERIALS

We have acquired and assembled the largest known collection of the endemic *P*. (*Poecilozonites*) from Bermuda, totaling over 350 samples now stored at the National Museum of Natural History (NMNH), Smithsonian Institution (SI) in Washington D.C. and the Field Museum of Natural History (FMNH) in Chicago. Our samples also include subsets from Stephen Jay Gould's collections from the Museum of Comparative Zoology (MCZ) at Harvard University. Gould-collected samples, prefixed by "SJG" in this study, are consecutively numbered, described, photographed, and vouchered in Gould (1969, "Register of localities, Appendix 2", p. 510). The Hearty and Olson *Poecilozonites* collections currently reside in the Bird Division at the SI. This location facilitated the collaboration of the authors over the past two decades in invertebrate and vertebrate paleontology, geology, and geochronology of Bermuda (see Olson et al. 2005). This snail collection will eventually be moved to the Division of Paleontology at the SI.

Many of the collections by Gould and ourselves predate the common availability of GPS devices but were faithfully recorded on topographic maps in that case. Where available, voucher numbers and GPS coordinates (and those approximated from Google Earth Pro®) are provided on collection sites (Table 2, Online Appendix 1, Online Supplemental File Fig. S1).

Approximately 450 shells, representing all morphologies and named species and subspecies of *P*. (*Poecilozonites*), were initially stratigraphically defined from their host stratigraphic setting (Table 1; Fig. 2) (Hearty et al. 1992; Vacher et al. 1995; Hearty et al. 2004; Olson et al. 2005; Hearty and Olson 2010) and additionally age-ranked with aminostratigaphy, ^{14}C and U/Th methods, yielding a high-resolution, well-ordered chronostratigraphy and phylogenetic succession.

This study will focus in detail on the stratigraphic and chronological succession since Termination II, the transition from MIS 6 to 5e and continuing to the present, highlighting paedomorphic occurrences and possible mechanisms during this interval. This interval of about 140 ka is particularly well represented geologically on Bermuda and in our collections.

SAMPLE MATERIAL

There are 14 samples from late Pleistocene MIS 5 deposits with *Poecilozonites* in Bermuda that contain paedomorphic (PAED) shell forms. About half of these sites were identified by Gould (1969; Table 2, Online Supplemental File Tab. S1). Over 68 sites with *P.b. zonatus* ZONA shells from the last interglacial (*sensu lato*) have been documented across Bermuda (Table 2, Online Appendix 1, Online Supplemental File Fig. S2A). Among our 350 collections are additional last interglacial PAED sites at Watford Island, Saltus School, Hamilton, Marsh Folly Road, and several sites on St. Georges Island including the Shell Oil depot (aka "Tank Farm"), Tobacco Bay, Wellington Road, Mullet Bay, and Government Hill (Table 2). The entire Holocene is represented by BERM, for which we have identified several new museum and field collections primarily from caves in the Walsingham district (e.g., Walsingham, Walsingham Sink, Fern Sink, Tom Moore's, Admirals, and Convolvulus Caves) (Table 2, Online Appendix 1). Older middle Pleistocene forms may also be classified as paedomorphs, such as *P. cupula triangularis* (TRIA of Hearty and Olson 2010), but the stratigraphic context and discussion of these is beyond the scope of this study as we have only few samples, and far less is known about paleoenvironmental conditions during the middle Pleistocene.

Shell measurements and photographs were taken of all reference collections and named taxa at the MCZ (Gould 1969) and compared with morphology and measurements of our own samples from which we established a definitive age and morphological correlation with "species" forms recognized by Gould (Online Appendix 2, Online Supplemental File Tables S1, S2). Specifically, for this study, we measured height (h) and width (w) with digital calipers to the nearest 0.1 mm on 333 complete, undamaged shells—and from these data calculated h+w, and h/w as a

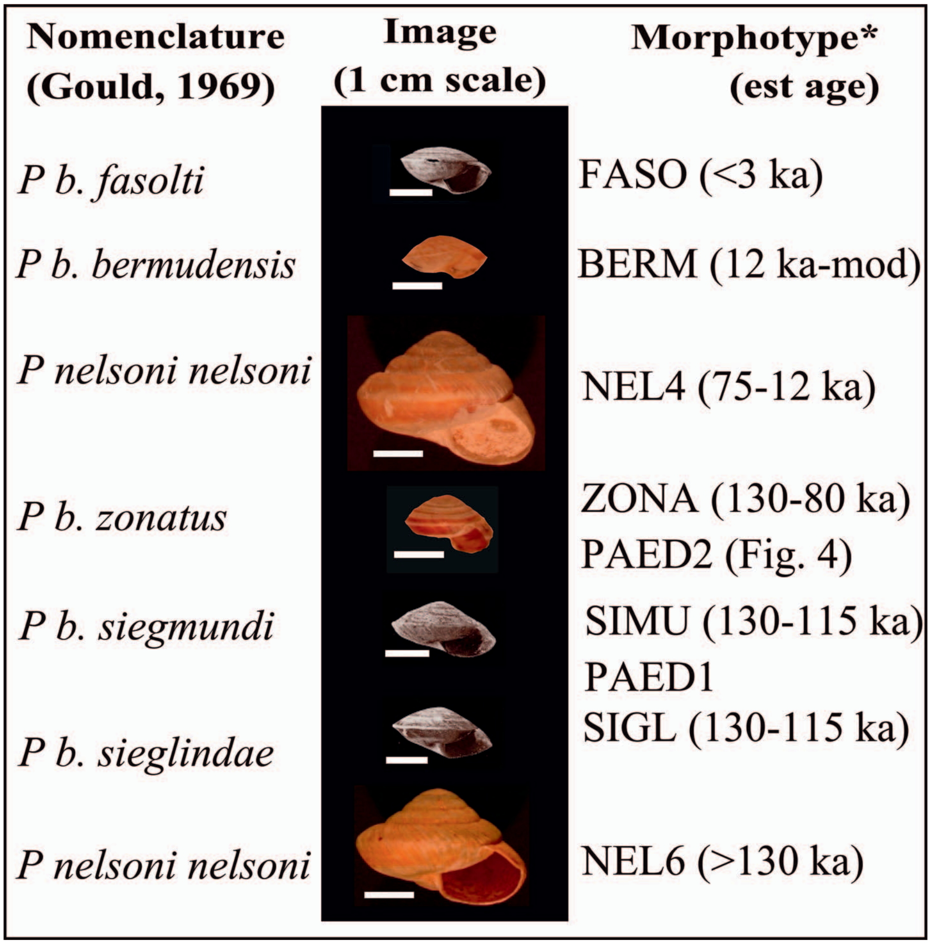

FIG. 2.—Morphological variation in *Poecilozonites* shells displayed in stratigraphic order from the end of MIS 6 (> 130 ka) to the present (approximate ages in parentheses). This "players list" shows the nomenclature used by Gould compared with morphotypes (with asterisk) adapted from Hearty and Olson (2010) and in this study. Voucher numbers for *P. b. fasolti*: MCZ28989; *P. b. siegmundi*: MCZ28990; *P. b. sieglindae*: MCZ28991 (Gould 1969, p. 506–510). Other collection information including available voucher number is provided in Online Appendix 1.

simple description of "total size" and "tallness or flatness" across the succession shell deposits. This simple morphometric test generally describes the groups previously identified by Gould as species and subspecies (Online Supplemental File Table S2). However, as we demonstrate, shell morphology is highly variable both within and between the sample collections, particularly among those containing paedomorphs. We initially suggest that this is probably not only factor of age, but more likely environmental changes within the habitat.

For AAR studies yielding relative ages, all *Poecilozonites* shells were sampled from precisely the same location on the shell at the growth edge of the aperture where it joins the previous whorl in order to minimize intrashell variation (Hearty et al. 2004). The epimerization ratio of D-alloisleucine /L-isoleucine (or A/I) was determined by ion-exchange (IE) on a high-performance liquid chromatograph (HPLC) at the Amino Acid Geochronology Laboratory (AAGL) at Northern Arizona University (D. Kaufman, Director). We restrict all AAR analyses and data in this study to the traditional IE-HPLC derivation of all samples yielding A/I values (Online Appendix 1).

In addition to the outcrop physical stratigraphy and superposition, AAR from three different sample materials (snails from soils and eolianites, marine shells from inter- and subtidal deposits, and whole-rock (WR) bioclastic sediment in past studies (Hearty et al. 1992, 2004) provides a multi-faceted geochronological framework in which comparison and ranking of land snails and their stratigraphic source deposits can be implemented. Independent age calibration of AAR ratios is provided at numerous sites by ^{14}C and U/Th ages from our mentioned studies on Bermuda and the previous work of others.

To avoid confusion with AAR notation (i.e., A/I), morphometric data are prefaced with "h+w" or "h/w"; for example: "h+w: 29.37 ± 1.24" and "h/w: 0.39 ± 0.03". AAR and morphometric sample analyses represent a spectrum or gradient of shell forms from PAED to typical ZONA (Online Appendices 1, 2).

RESULTS

Morphometric Analysis of Paedomorphic Shells

Rapid shell form transitions since the penultimate glacial and particularly at MIS boundaries (Fig. 3) are evident from the morphological data. Simply stated, larger and taller shells dominate during and at the close of cold glacial periods, and much smaller and flatter shells are prevalent at the onset of and during warm interglacials (i.e., MIS 6 to 5e; MIS 5d/b to 5a; MIS 2 to 1) (e.g., Bergmann 1847). Figure 3 reveals the general stratigraphic progression associated with changing shell forms since the end penultimate glacial (MIS 6/5e), while certain strongly paedomorphic groups are indicated by the arrows.

TABLE 2.—*Study sites (see Online Supplemental File Figs. S1, S2) including sample names, cross-referenced with Gould (1969) associated morphotypes, site names, and GPS coordinates. Refer also to Olson et al. (2005) for additional information on cavernous fossil sites.*

Loc. #	Sample name	Morphotype	Site name and Gould (1969) site number if same probable location	GPS decimal coordinates (approx. collection location) Lat. °North × Long °West
1	Level xy	BERM	Admirals Cave	32.351556 -64.713333
2	USNM1	BERM	Cockroach Island at Abbott's	32.335797 -64.734114
3	UWV1	BERM	Walsingham Cave SJG53	32.348528 -64.710555
4	UWS1	BERM	Walsingham Sink SJG5	32.348138 -64.710833
5	UGP1z	BERM	Grace Island	32.273126 -64.835515
6	UGC1x/z	BERM/FASO	Fern Sink SJG53	32.347472 -64.712778
7	SJG53	BERM	Gould's Tom Moore's SJG53	32.346726 -64.708511
8	UVV1-3	BERM	Convolvulus Cave	32.351806 -64.71278
12	UII1	PAED/SIMU	Ireland Island SJG10	32.313615 -64.847764
17	UGQ	ZONA	Government Quarry SJG5	32.341480 -64.705857
19	USH	ZONA	Saucos Hill SJG39-41	32.305894 -64.734862
20	UCO	ZONA	Conyers Bay	32.271202 -64.880856
21	USE1a/b	ZONA	Sonesta Beach Hotel	32.275843 -64.776993
22	UML3	PAED	Mullet Bay site 3, N=20	32.379290 -64.688012
23	UMG1	ZONA	McGall's Bay (South Shore Rd)	32.311337 -64.733186
24	UTB2a/b/	BERM	Tobacco Bay West SJG27	32.389007 -64.678778
25	SJG27	PAED	Tobacco Bay; Fort St. Catherine	32.388080 -64.678398
26	UAP1e	ZONA	Astwood Park	32.264388 -64.800625
27	UKN2b	COID	Knapton Hill	32.317005 -64.720704
28	UWK;WLB1b	ZONA	Warwick Long Beach	32.355717 -64.716562
29	UCH1b	ZONA	Charles Island; SJG55	32.338533 -64.671768
30	UWI	ZONA	Windsor House	32.335390 -64.682066
31	UAS1c	ZONA	Ariel Sands	32.297455 -64.747049
32	UWT1b	ZONA/PAED	South end, Watford Island SJG66	32.305422 -64.857170
33	UDB1/URB	ZONA/SIGL	Devonshire Bay/Rocky Bay SJG2/44	32.298241 -64.745059
34	UCV	ZONA	Convict Bay	32.344901 -64.733562
35	UWB	ZONA	Whalebone Bay SJG1	32.365322 -64.713872
36	"U"BWP1b/2a	ZONA	Marsh Folly Rd at Blackwatch Pass SJG6	32.301934 -64.784585
37	USL1d/UFE2	ZONA/PAED	Shell Depot, Tank Farm, SJG11/DHL	32.371988 -64.700712
38	UCOY1b	ZONA	Near Coney I; SJG68	32.357484 -64.714414
39	UOL1 c	ZONA	Radnor Rd and North Shore Rd	32.334498 -64.732986
40	UAB1d	ZONA	Albuoy Point,	32.367699 -64.649052
41	UBU1b	ZONA	North Shore NE of Flatts at Burschell Bay	32.336618 -64.738693
42	ULV2bc	ZONA/PAED	Love Lake east of Whalebone Bay	32.366134 -64.711624
43	UHO1g	ZONA	Above Horseshoe Bay in roadcut	32.252978 -64.823741
44	UHR1	ZONA	Harvey Road, upper, N=10	32.311549 -64.749507
45	UBW1	ZONA	Blackwatch Pass	32.303296 -64.785218
46	USS1	PAED	Saltus School	32.303784 -64.861910
47	USC1c	ZONA	South Court Ave; South Shore	32.298044 -64.865077
48	ULA	ZONA	Laffan St, Hamilton	32.297548 -64.786293
51	UFL1c	ZONA/HYBR	Flatts Bus stop; SJG3	32.327013 -64.742104
69	UNSM1072295	BERM	Hamilton; collected live	No GPS data
70	UNSM 522500	BERM	Flatts; collected live	No GPS data
71	USP1	BERM	Spittal Pond dredging	32.311309 -64.725789
72	UWE1	PAED1	Wellington Rd, St. Georges	32.379519 -64.688563
73	URI	BERM	Rat Island, Harrington Sound	32.332997 -64.729248
74	UGV	PAED	Government Hill, St. Georges	32.384223 -64.676580

Specimens identified as paedomorphs exhibit flatter, low-domed shells with distinctly carinate whorl margins, compared to contemporaneous ZONA (Fig. 4). The orange horizontal bands in Figure 4 represent glacial-age *terra rossa* palaeosols, contemporaneous with the larger form NEL6 (MIS 6) and NEL4 (MIS 4-2) shells.

Size distribution h+w peaks of paedomorphs ranges between at 15 and 35 mm (Fig. 5A), with a modal group between 24 and 32 mm. Similarly, a frequency plot of h/w of 333 shells (Fig. 5B) displays a normal Gaussian distribution between h/w 0.30 and 0.50. An h/w of 0.42 arbitrarily defines a boundary between PAED (h/w: 0.35 to 0.41) and ZONA (h/w: 0.42 to 0.50+) (Figs. 3, 5B). If a large number of shells representing ontogenetic stages between juvenile (smaller, flatter shells) and adult (larger, higher-domed shells) were typical among sampled shells, there should be a positive correlation between size and height. An $r^2 = 0.11$ (Fig. 5C) indicates that no such correlation exists in the fossils. In Figure 5D, we plotted the size and height of a living population of juveniles to adults (Outerbridge data and personal communication), and from that comparison, determined a positive correlation of $r^2 = 0.64$, reinforcing our procedures for selection of primarily adult fossil shells as sample material.

Samples from two successive protosols of similar age located within meters of each other at Rocky Bay show a broad h/w range of variation [h/w: 0.27–0.49] between PAED1 and ZONA (URB1c; URB1d in Figs. 4J,

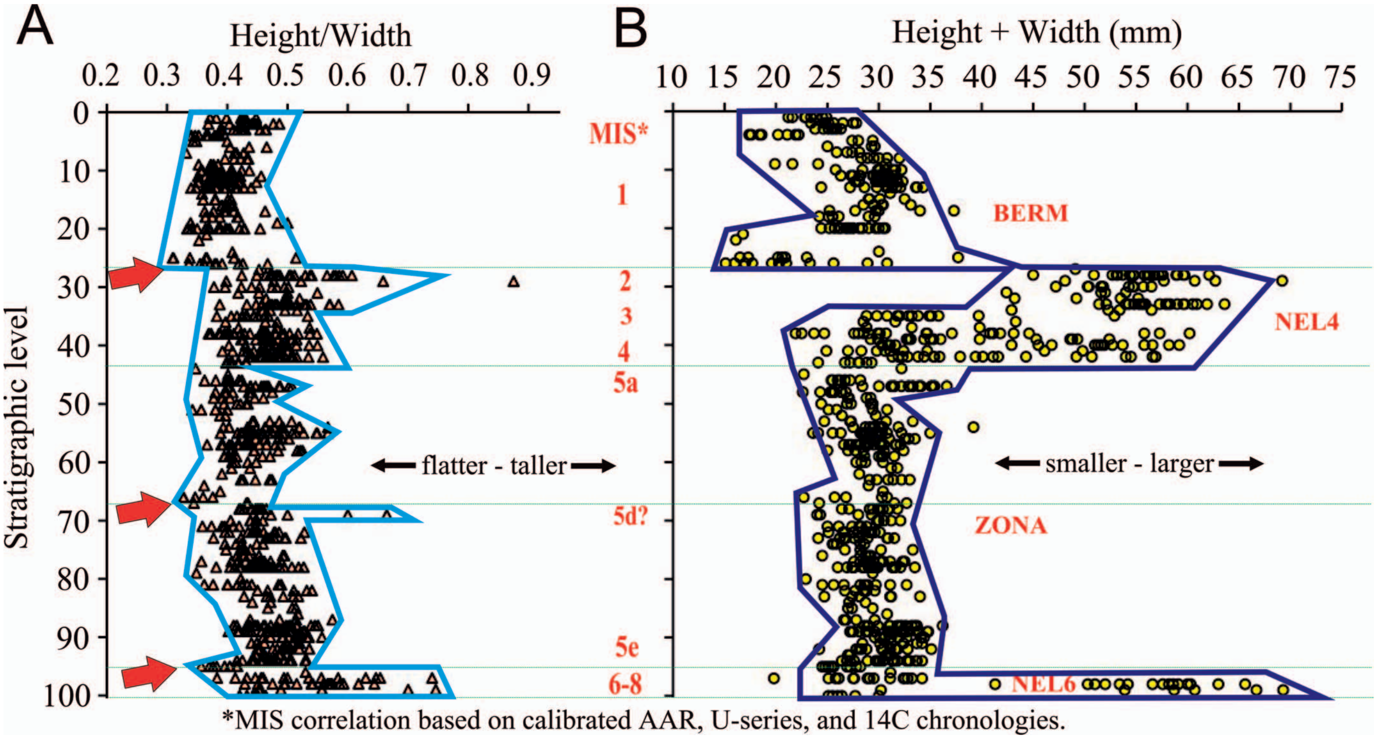

FIG. 3.—Morphometric data and stratigraphic plots. **A**) Shell height/width (h/w). **B**) Shell height + width (h+w) in shells since the penultimate glacial stage (MIS 6-8). Arrows indicate Intervals where paedomorphism is most pronounced. Stratigraphic level is a function primarily of the stratigraphic age of the source deposits of the fossils, and secondarily on the AAR value of the sampled shells (see Hearty and Olson 2010).

4K, 4N; Online Appendix 2). PAED1 in central and western parts of Bermuda are generally slightly larger than PAED2, which are known only from St. Georges (Fig. 4D1–4F). The older PAED1 are slightly but not statistically flatter than PAED2, whereas the PAED1 and PAED2 on St. Georges are indistinguishable from each other. On St. Georges, it is not certain if PAED1 and PAED2 are separate iterations or if the morph lasted the entire duration of MIS 5 interglacial (130–80 ka), as only early and late fossil-bearing stratigraphic exposures from this interval are known from this area.

The oldest and earliest Holocene BERM shells (Figs. 3, 4AB) are considerably smaller (h+w: ~20 ± 5 mm) than those from later in MIS 1 associated with cave sites near Tom Moore's Tavern (h+w: ~30 ± 3 mm). Several of the recent live-collected and surface dead collections (Fig. 3, Online Appendix 2) also show a trend toward smaller shells (h+w: 22 ± 3 mm), which may be due to predation pressure from exotic organisms (rats, pigs, predatory snails, etc.) and human impact on the natural environment over the past several centuries since Bermuda's discovery by Europeans in 1505 AD.

Although BERM (*P. bermudensis*) was thought to have been extinct since before the 1960s (Gould 1968, 1991; Bieler and Slapcinsky 2000), a remarkable discovery of a small living population (> 300 juvenile to adult individuals) was recently made near Front Street in downtown Hamilton, Bermuda (Outerbridge 2015; Outerbridge and Sarkis, 2018).

Stratigraphy and Geographic Distribution of Paedomorphs

General.—All PAEDs yield A/I values between 0.40 to 0.60, which bracket Aminozone C, D, and E, equivalent to that for ZONA (Fig. 6, Online Appendix 1). This interval encompasses the full last interglaciation (MIS 5 *sensu lato,* 130–80 ka) in both surface and cave deposits (Hearty et al. 1992, 2004; Hearty 2002; Hearty and Olson 2010; Table 1, Online Appendix 1). Within this time frame, 60% of PAED1 shells yield higher (older) A/Is between 0.53 and 0.60+. The balance of values from the PAED2 group is associated with A/I of ~ 0.40. It is important to note that at all MIS 5 PAED collections that we examined, there was a small to dominant percentage of intermixed taller ZONA morphs.

PAED1.—PAED1 thus correlates with early MIS 5e and Aminozone E (Hearty et al. 2004), independently dated by various methods between approximately 130 ka and 118 ka (Harmon et al. 1983; Ludwig et al. 1996; Hearty et al. 2004). The PAED1 sites at Rocky Bay (URB), including Gould's *P. b. sieglindae* (SJG44), originate from the uppermost units of the Rocky Bay Formation (south coast, central Bermuda), corresponding stratigraphically with late MIS 5e, around the time of, or shortly after, a maximum sea-level high stand of +9.2 m recorded at Spencer's Point (Land et al. 1967; Hearty 2002; Hearty et al. 2007). Many of the shells are positioned just at the upper limits of a marine unit upon which the Harrington soil has developed. This succession and soil are locally buried by the younger eolianite of the Hungry Bay Fm. (Hearty 2002). Shells corresponding with Gould's SJG44 (Rocky/Devonshire Bay), yield an aggregate A/I mean of 0.54 ± 0.06 (6). Similarly, the PAED1 that Gould's (1969) named *P.b. siegmundi* (Ireland Island in westernmost Bermuda; SJG10) yields an equivalent aggregate A/I mean of 0.54 ± 0.03(9). Our two PAED1 from an eolianite-bracketed, light colored soil at Saltus School (our site #46 in Hamilton) and the Shell Oil Depot (site #37 Tank Farm; St. Georges) have mean A/Is of 0.59 ± 0.02 (3) and 0.54 ± 0.05 (3), respectively. Thus, all the above distinctly Pleistocene paedomorphic forms including those named by Gould (1969), equate with the last interglacial Aminozone E and exist stratigraphically in the latter half of MIS 5e (~ 123–118 ka?).

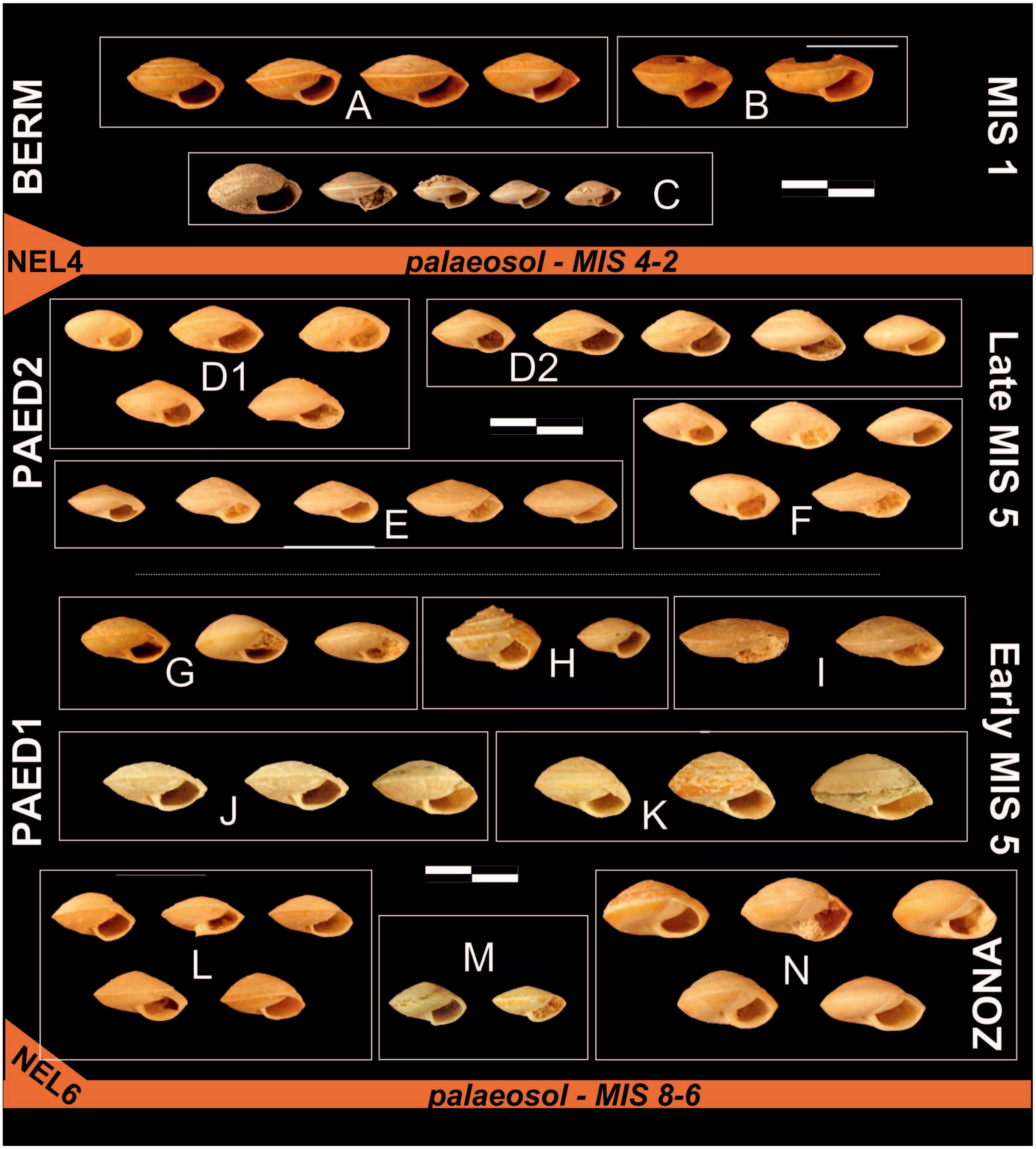

FIG. 4.—Images showing representative specimens of ZONA, PAED1, PAED2, and BERM from several localities around Bermuda. Scale bar = 2 cm. **A**) BERM from UGC2z (Grand Canyon Cave). **B**) SJG53 (Tom Moores Cave). **C**) A(4x0)x (Admirals Cave). Note: Field numbers in this format "A(4x0)x" are 3-dimensional coordinates of samples excavated from cave sites. **D1**) PAED2 from UTB (Tobacco Bay). **D2**) PAED2 from SJG 27 (Gould collection at Tobacco Bay). **E**) UML (Mullet Bay 1). **F**) UML3 (2 Mullet Bay 2). **G**, **H**) PAED1 from UFE2cd (lower) and UFE2e (upper) (2 strata from DHL warehouse on Ferry Road. **I**) PAED1 from USL (Shell Oil Depot, aka Tank Farm). **J**, **K**) URB1c (lower) URB1d (upper) (2 successive collections at Rocky Bay). **L**) PAED1 at USS1c (Saltus School in Hamilton). **M**) PAED1 at UWT1b (Watford Island in western Bermuda). **N**) typical MIS 5e ZONA at SJG17 (near Whalebone Bay, St. Georges). Glacial age reddish palaeosols (MIS 8-6 with NEL6 and MIS 4-2 with NEL4) are represented by the orange horizontal bars.

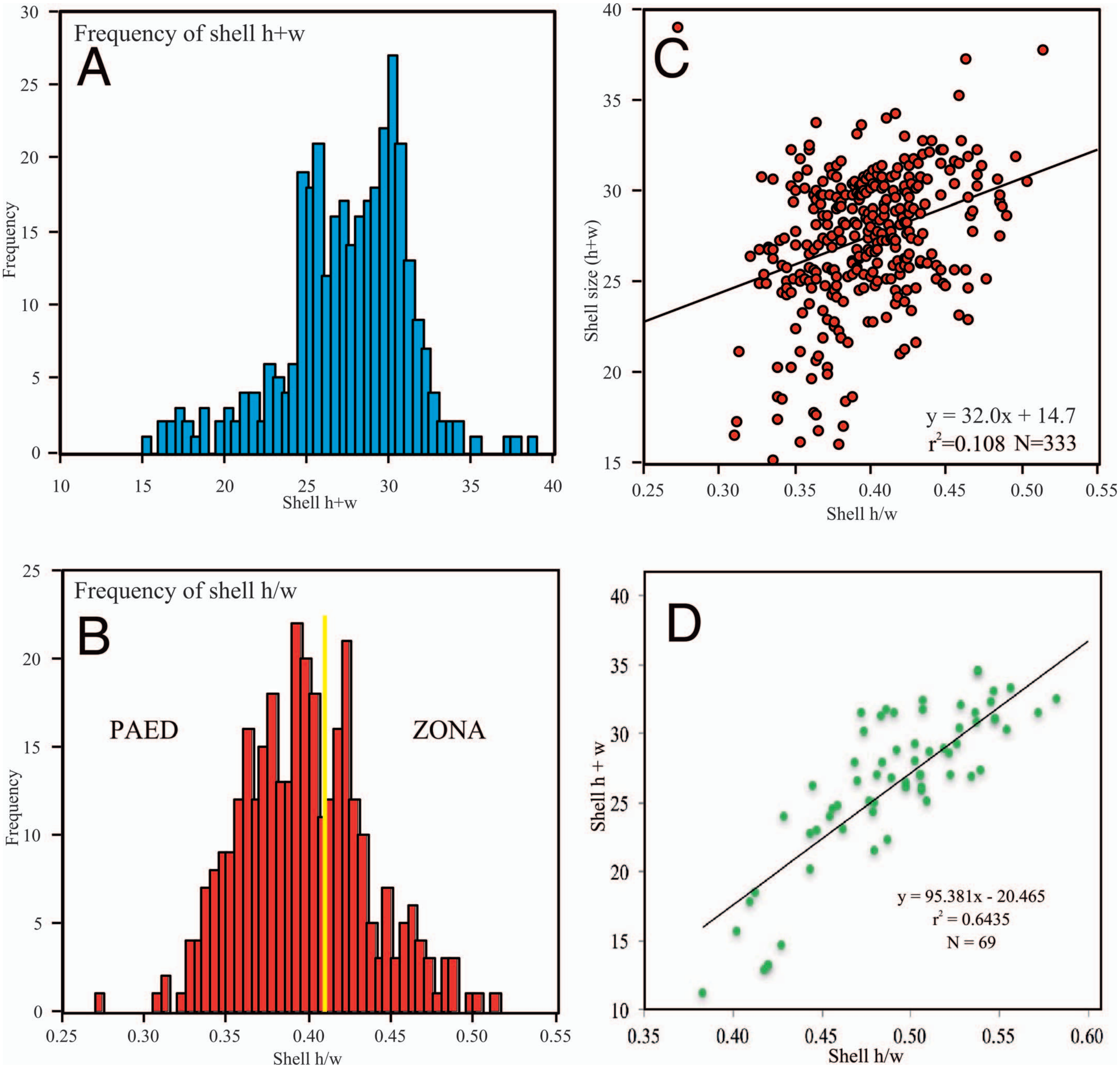

FIG. 5.—Shell size and shape of *Poecilozonites*. **A**) A plot of shell size (h+w; size) shows the modal size of shells generally between 24 and 32 mm. **B**) Frequency diagram showing the distribution of shell height/width (h/w; flatness versus tallness) in 333 shells. An arbitrary cutoff between PAED and ZONA is 0.42. **C**) A plot showing the relationship between shell size (h+w) and shell tallness (h/w) in 333 shells. The r^2 value of 0.108 indicates there is only weak correlation between shell size and shape as would be expected if an ontogenetic gradient of shells from juveniles to adults were being analyzed. **D**) Plot of the size and height of a group of newly discovered living population of 69 juveniles to adults *P. bermudensis* shells (Outerbridge data and personal communication), and from that comparison, a strong positive correlation of $r^2 = 0.64$ was determined, reinforcing our procedures for selection and use of primarily adult fossil shells as sample material.

PAED2.—Three PAED2 shells from sites exposing white protosols in eolianites of the Southampton Fm. (Table 1) in St. Georges Parish yield an average A/I of 0.40. Both Gould's and our numerous sites around Tobacco and Mullet Bays on St. Georges are associated with Aminozone C of Southampton age, correlated with MIS 5a (Vacher and Hearty 1989; Hearty et al. 1992) around 80 ka ago. St. Georges localities contain both PAED1 (Shell Depot; some Mullet Bay sites, and Wellington Road) and PAED2 (Tobacco and some Mullet Bay area) (Fig. 4D) corresponding with exposures of Rocky Bay and Southampton eolianites (Vacher et al. 1989), respectively. Thus, from stratigraphic and AAR data, we establish that all PAED1, PAED2 and ZONA shells from all collections occurred within a 50-ka interval of the last interglacial period from about 130 to 80 ka in agreement with previous works including Admiral's Cave (Hearty et al. 2004). The PAED1, PAED2, and ZONA bearing strata are bracketed

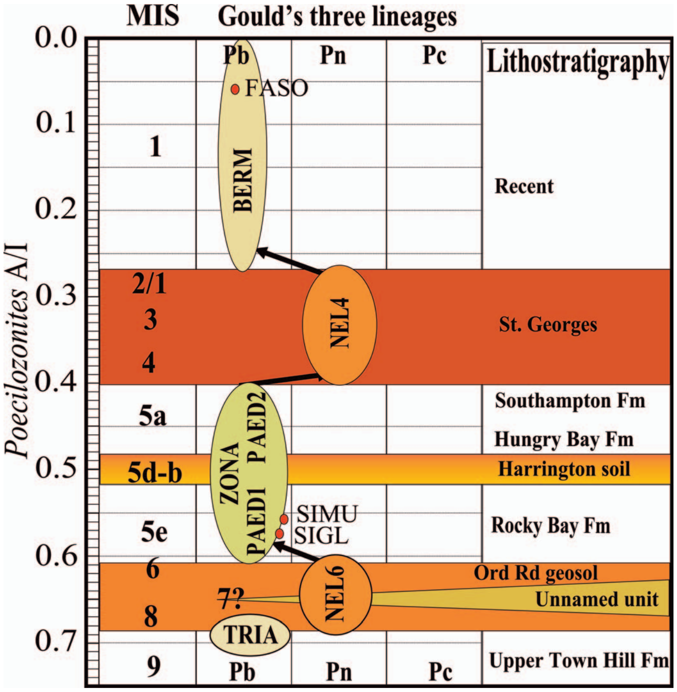

FIG. 6.—Stratophenic chart showing the trajectory and occurrences of morphotypes of *Poecilozonites* over the past ~ 150 ka. Approximate amino acid values are provided in the y-axis (Online Appendix 1). We demonstrate that NEL6 gave rise to both PAED and ZONA, while NEL4 was the sole progenitor of BERM. This study indicates that the three species lineages of Gould (1969) and Eldredge and Gould (1972) identified in central columns (Pb = *P. bermudensis*; Pn = *P. nelsoni*; Pc = *P. cupula*) did not coexist at any time during the late Quaternary. A schematic comparison of Gould's (1969) plot versus ours is shown in Online Supplemental File (Fig. S4).

on both the older and younger transitions by NEL6 and NEL4, respectively.

NEL4 to BERM.—NEL4, *P. nelsoni* was determined to be the only morph on the island between 70 and 10 ka (MIS 5/4 to 2/1; Figs. 3, 6). In a biologically unmixed continuous stratigraphic and age-constrained talus pile of Admirals Cave (Hearty et al. 2004), the giant form NEL4 disappears at a sharp boundary at the beginning of the Holocene and BERM immediately dominates thereafter as the exclusive morph. There is no alternative explanation other than BERM is the obvious and exclusive derivative of NEL4 at the MIS 2/1 glacial to interglacial transition, which occurred over as little as 3 ka as constrained by ^{14}C ages on charcoal and shells (Hearty et al. 2004) (Table 1, Online Appendix 1).

BERM.—BERM localities occur across Bermuda but are best represented in caves and fissures in the Walsingham District (Table 2, Online Supplemental File Fig. S2C). Our Holocene collections in the area of Gould's "Tom Moore's Tavern" include shells from Walsingham Cave, Walsingham Sink, and Fern Sink Cave (Table 2). We are certain that one of these sites is Gould's (1969) "Tom Moore's Cave" site (SJG53), as all three are situated within a hundred meters of the Tavern. The shells are commonly embedded in red clayey soils that appear to have been transported along with the shells into the caves from the overlying middle and early Pleistocene landscapes. The clays are old, but the intermixed snails and charcoal are far younger as surface deposits. Unfortunately, introduced predators and human activities are probably responsible for the nearly complete disappearance of BERM fossils and shells from the modern landscape, even as surface dead.

One of three shells averaging A/I = 0.05 ± 0.01 (3) from Fern Sink Cave (site #6) produced an AMS ^{14}C age of 1520 ± 70 cal yr BP (Hearty and Olson 2010). A sample of *P.b. fasolti* (our FASO) from Gould's MCZ collection from "Tom Moore's Tavern Cave" produced nearly identical morphometrics (Online Appendix 2) and A/I values of 0.06 ± 0.03 (2) (Online Appendix 1) compared with Fern Sink and other BERM shells from the caves in the area. Thus, the A/I and ^{14}C ages indicate that Gould's *P.b. fasolti* must be late Holocene and no more than 2–3 ka old, despite his previous interpretation of an age of ~ 300 ka. The association of *P.b. fasolti* with deep-red clayey colluvial sediment may have influenced Gould to correlate them with much older Shore Hills Soil deposits.

With the recent rediscovery of living *P.b. bermudensis* (BERM) in Hamilton (Outerbridge 2015; Online Supplemental File Fig. S3 poster), both *P. b. bermudensis* and *P.* (*Discozonites*) *circumfirmatus* are being protected and propagated at the Bermuda Aquarium, Museum, and Zoo (BAMZ) and the Zoological Society of London with the intent of future reintroduction to isolated, pest-free areas of Bermuda (Lines 2002; Sarkis 2009; Outerbridge and Sarkis 2018), which may include offshore islands cleansed of introduced predators.

DISCUSSION

Fragmentation of Poecilozonites *Populations by Sea-Level Rise*

What were the environmental conditions surrounding the reversible changes in shell morphology in *Poecilozonites* at end-glacial Terminations II and I? All populations of PAED are correlated explicitly with the last interglacial MIS 5 and the timing and co-occurrence with ZONA, whereas those of BERM and FASO are Holocene. Presumably, if multiple distinct lineages coexisted beyond glacial-interglacial cycles on Bermuda, those forms would be found mixed in some of the more than 100 known fossil exposures on Bermuda (Hearty and Olson 2010) representing most of the past 500 ka (Hearty and Olson 2010). The odds of finding mixed populations would be particularly high in deposits correlating with interglacial highstand cycles, when all the terrestrial organisms were concentrated on exponentially smaller land areas. Evidence of these sea-level driven snail concentrations is now preserved in the great shell abundances in pitfall deposits such as Admiral's Cave and Fern Sink (Hearty et al. 2004; Olson et al. 2005).

At the end of the penultimate deglaciation (MIS 6), with the rise of MIS 5e sea level, vast areas of the 650 km^2 Bermuda platform were flooded that may have been partially or fully exposed for perhaps as long as ~ 150 ka (~ 280 to 130 ka). As sea level rose above the platform margin at (-20 to -30 m) depth during the MIS 6/5e deglaciation, the flatlands were rapidly flooded and topographic highs of "Older Bermuda" (Sayles 1931) were progressively isolated as smaller islands. With sea level positioned between +2.5 m and +9 m (Hearty et al. 2007; Kopp et al. 2009; O'Leary et al. 2013), land areas far smaller than the current total island area of ~ 56 km^2 were isolated by seawater channels.

With the onset of Termination II (MIS 6/5e) NEL6 (Hearty et al. 2007), the prevalent 'giants' of the penultimate glaciation(s), were progressively concentrated into much smaller land areas. Corresponding with a reduction in land area by at least an order of magnitude, there was a rapid transition from NEL6 to the smaller morphs of ZONA and PAED in early MIS 5e, reflected in the biostratigraphy of Admiral's Cave. Fragmentation of the Bermuda platform by rising seas would have isolated smaller populations, while increasing faunal densities and competition for reduced food resources, as Goodfriend (1986) found with many species of land snail. More limited resources would presumably result in slower growth rate of the paedomorphic forms. Organic amino acid concentrations are generally greater in the giant NEL4, compared to smaller ZONA and PAED (Hearty and Olson 2010), perhaps reflecting a more luxuriant environment. Further, Gould (1969, p. 506–510) provides some fundamental but sketchy data to support this hypothesis, indicating that BERM and PAED produced generally 5–6 post-protoconch whorls, while NEL6/4 generally produced 7–8. Gould's averages from numerous lots were based on apparently about 5–20 specimens each. His data appear to generally support our position that reduction in adult land snail body and shell size would offer ecological advantages to deal with decreased food supply and quicker reproduction.

A strong maritime influence in the terrestrial ecosystem would further increase environmental stresses by reduction of vegetation and fresh water, with increased UV exposure and salt spray. Smaller islands would simultaneously have experienced a decrease the number and diversity of predators (Olson and Hearty 2010) by decreasing the range of habitats, along with dramatic compositional changes in the plant communities (Olson 2008).

Over 68 sites containing ZONA shells from the last interglacial (*sensu lato*) have been documented across Bermuda (Hearty and Olson 2010; this study) (Online Appendix 2, Online Supplemental File Fig. S2A). Yet, only a few PAED1 collections from interglacial protosols are known from the central and western parts of Bermuda (Online Supplemental File Fig. S2B). The more elevated mid to early Pleistocene landscape of "Older Bermuda" (Sayles 1931) consists of soil-mantled indurated eolian dunes formed during Walsingham and Town Hill times (Vacher et al. 1989). These +10–40 m hills of "Older Bermuda" (Fig. 1) may have offered larger and more stable *refugia*, perhaps with well-developed soils and a mix of forest, grassland, and ephemeral fresh water lenses perched on clayey soils. Rising seas would have had less direct impact in these higher areas, and for this reason, we suggest that paedomorphosis was less common in Older Bermuda due to reduced environmental stress compared to lower elevation landscapes. While normal-domed ZONA shells occurred across parts of Older Bermuda, PAEDS appear to have emerged lower parts of the platform subject to partial inundation and more direct maritime influence during highstands.

The stability of PAED1 and PAED2 forms associated with eolianites on St. Georges Island may perhaps be due to sustained terrestrial isolation during much of MIS 5 (~ 130 to 80 ka), much like the Holocene. Active marine channels flowing across the eastern part of Bermuda may have persisted for much of early MIS 5, particularly during later MIS 5 (Vacher and Hearty 1989).

The transition from NEL4 to BERM around 13–12 ka appears to have been initiated with a major climatic and ecological fluctuation perhaps keyed to the Younger Dryas (warming, sharp cooling, then warming) (e.g., Broecker et al. 1989; Dansgard et al. 1989; Keigwin 2004) and subsequent post-glacial sea-level rise. Gould's (1968, 1969) *P.b. fasolti* (FASO) was a latecomer with an age of about 2–3 ka and is equivalent to our BERM, which survives today.

CONCLUSIONS

Advances in our understanding of the physical stratigraphy and geochronology of Bermuda have established the proper biostratigraphic order and ages of the endemic land snail *P.* (*Poecilozonites*). The penultimate glacial giant NEL6 is the progenitor of both ZONA and PAED in the transition of MIS 6 to 5e. These morphs persisted throughout the MIS 5 interglacial, then again reverted to the giant NEL4 at the onset of the last glacial cycle from MIS 4 to 2. At the beginning of the Holocene, the smaller paedomorphic form BERM emerged, and has dominated until present.

Our studies reveal that many essential elements of Eldredge and Gould's phylogeny (Online Supplemental File Fig. S4) supporting PE from Bermuda were either out of stratigraphic order or inaccurately dated. PAED1 morphs (including Gould's "species" *P. b. siegmundi* and *P. b. sieglindae*) co-existed locally with ZONA only during the last interglaciation (MIS 5), while Gould's *P.b. fasolti* is not 300 ka as he proposed, but < 3 ka. Despite multiple iterations of giants and paedomorphs since the penultimate glaciation, it is evident that new species did not result.

We suggest that the extreme concentration of land organisms into progressively smaller island areas by sea-level rise created adverse ecological conditions except at higher elevations, leading land snails to revert to a more reproductively/metabolically efficient state through paedogenesis, which would allow smaller snails to eat less, grow less, and reproduce more efficiently, providing an ecological "foot-up" for survival in the harsh environments of low-lying oceanic islands during intense sea-level changes.

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In his "*Time's Arrow Time's Cycle*" (1987), Stephen Jay Gould wrote these words of encouragement in 1989 to Hearty: "*In expectation of resolving time's arrow on Bermuda.*" We pay homage to S. J. Gould (1941–2002) for his pioneering work in evolutionary theory and hope that we have advanced "time's arrow" a bit forward. In Bermuda, we thank Robbie Smith, Wolfgang Sterrer and Lisa Green, Bermuda Aquarium, Museum and Zoo (BAMZ) for their enthusiastic support of our research and David B. Wingate, Jeremy Mederios, and Frederick V. Grady for participation in the field. Special thanks to Bruce Lines, his son Alex, and Mark Outerbridge (Conservation Services) for permission to show his poster, and for shared details about the recently discovered living population of *P. bermudensis*. Our studies have been made possible by the long-term cooperation and support of the Bermuda Government, particularly staff and facilities at the Bermuda Aquarium Museum and Zoo. Fred Collier facilitated our subsampling of Gould's collections, while K. Burns measured Gould's specimens during our work in the MCZ at Harvard University. The Bermuda Ministry of the Environment, the Alexander Wetmore Fund of the Smithsonian Institution, intramural support from James Cook University (Queensland), and a multi-year Queensland-Smithsonian Fellowship (2001–2003) to PJH generously provided funding for fieldwork and many of the AAR and ^{14}C analyses. The AAGL at Northern Arizona University (D. Kaufman, Director) provided AAR data. We are grateful to the editors, an anonymous reviewer, and G. Vermeij for their constructive comments which greatly improved the manuscript. This is Contribution #272, Bermuda Biodiversity Project (BBP), Bermuda Aquarium, Museum and Zoo, Department of Environment and Natural Resources.

SUPPLEMENTAL MATERIAL

Online appendices and supplemental data are available from the PALAIOS Data Archive: http://www.sepm.org/pages.aspx?pageid=332.

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