LONG-TERM ASSOCIATION BETWEEN THE COMMENSAL FLORIDA MOUSE (*PODOMYS FLORIDANUS*) AND THE GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) IN THE FOSSIL RECORD OF FLORIDA

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ABSTRACT

The Florida Mouse *Podomys floridanus* and the Gopher Tortoise *Gopherus polyphemus* are linked in modern ecosystems by a commensal relationship in which *Podomys* uses the burrows of *Gopherus*. However, previous paleoecological research demonstrated that species interactions, including commensalisms, are not necessarily stable through geologic time. Given that the longevity of species interactions cannot be assumed, we asked: is the current association between *Podomys* and *Gopherus* a coincidental feature of the modern biota or is it a long-term phenomenon detectable in the fossil record? We explored that question using literature and collection records of *Podomys* and *Gopherus* from throughout the published geographic and temporal extent of the fossil record of *Podomys* (Florida, ~1.35 Ma – 0.01 Ma). We expected that a long-term commensal relationship would result in the presence of *Gopherus* in sites preserving *Podomys* significantly more often than expected by chance. Given the asymmetric nature of the relationship, a complementary expectation is that a search for sites containing *Gopherus* within the same spatiotemporal extent should not result more sites containing both species than would be expected by chance. After accounting for potential collection biases, fourteen Irvingtonian and Rancholabrean sites preserving *Podomys* were searched for occurrences of *Gopherus* as well as other vertebrates whose burrows *Podomys* is reported to use. Twelve of those fourteen sites contained fossils of *Gopherus*. The two remaining sites contained fossils of the other candidate taxa, consistent with the hypothesis that if *Podomys floridanus* did not use the burrows of *Gopherus*, it could have used the burrows of other species, as it does in modern ecosystems. Among the sites that are from the same spatiotemporal extent and contain *Gopherus*, fossils of *Podomys* were no more likely to be present at a site than would be expected by chance. Overall, we find evidence that *Gopherus* and *Podomys* have a long-term association consistent with their current relationship that extends at least to early Irvingtonian faunas.

Key words: ecology, Gopher Tortoise, Florida Mouse, Pleistocene, Rancholabrean, Irvingtonian.

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INTRODUCTION

The fossil record contains data that extend our understanding of the stability of ecological associations. A key insight from paleoecological research is that, despite the faunal stasis that is prevalent in the fossil record (Morris et al., 1995; McGill et al., 2005; Blois and Hadly, 2009; Gill et al., 2009), the responses of individual species to climate change leads to no-analogue communities through time (e.g., Hoffman, 1979; Stewart, 2008). Those same no-analog assemblages demonstrate that species distributions can change through time, and that two species currently in syntopy may not represent a long-term sympatric association (Semken Jr, 1983; Graham, 1986; Davis et al., 2014).

Species pairs linked by ecological interactions such as mutualism, parasitism or commensalism might be predicted to be more closely associated through geologic time than ecologically unassociated pairs from a community (Wilf et al., 2000). However, even ecological associations between species pairs are subject to change over time. For example, the 'obligate' predator-prey relationship between black-footed ferrets and prairie dogs may have emerged within the last 800,000 years, as black-footed ferrets colonized areas of North America containing prairie dogs (Owen et al., 2000). Therefore, study of the fossil record of species pairs is a potentially powerful way of understanding the evolutionary stability of such relationships.

An example of such a species pair is the Florida Mouse (*Podomys floridanus*, hereafter *Podomys*) and the Gopher Tortoise (*Gopherus polyphemus*, hereafter *Gopherus*) in peninsular Florida. *Podomys* has an asymmetric, commensal relationship with *Gopherus* in which *Podomys* benefits from the presence of *Gopherus* but *Gopherus* is unaffected by the presence of *Podomys*. *Podomys* has been characterized as exclusively burrow-dwelling (Layne and Jackson, 1994). Unlike the sympatric *Peromyscus gossypinus*, which also utilizes large burrows dug by other animals, *Podomys* is a poor burrower itself and is considered to be specialized for burrow-dwelling, as opposed to burrow-excavation, due to its limited burrowing ability, weaker nest-building behavior (Layne and Jackson, 1994), and physiological traits that make burrow-dwelling a key for its specialized xeric habitat (Fertig and Layne, 1963). *Gopherus* was previously described as an ecosystem engineer due to its excavation of prominent burrows that can be re-engineered by *Podomys*, which uses the main burrow or digs rudimentary small pockets and escape chimneys off of the main burrow (Jones and Franz, 1990; Kinlaw and Grasmueck, 2012). *Podomys* prefers the burrows of *Gopherus* to those of other species (Blair and Kilby, 1936; Jones and Franz, 1990; Layne, 1990; Layne and Jackson, 1994) but has also been observed entering burrows of other animals such as *Peromyscus polionotus, Sigmodon hispidus*, *Geomys pinetis*, and *Dasypus novemcinctus* (Layne, 1990).

It is unclear when burrow-associated behavior evolved in the ancestors of *Podomys* and *Gopherus*. It may be related to the extension of a xeric province along the northern Gulf of Mexico, which would have been followed by an eastward range extension of the ancestors of *Podomys*, *Gopherus*, and other scrub associated biota from the American southwest (5–2 mya; Axelrod, 1948; Myers, 1990; Haywood et al., 2001; Reynoso and Montellano-Ballesteros, 2004). Alternatively, *Podomys* may have evolved as a xeric specialist during the Pleistocene when major ecological changes occurred in peninsular Florida, including the formation of much of the current xeric scrub ridges (Myers, 1990). The applicability of a phylogenetic bracket to infer the evolution of burrow-association is limited because the evolutionary relationships of *Podomys* to other neotomine species remain unresolved (Bradley et al., 2007; Platt et al., 2015). It is also possible that a xeric habitat association alone may explain an association between the two taxa in the fossil record without the need to infer burrow-association.

The longevity of the association between *Gopherus* and *Podomys* can be studied in the fossil record. Here, we use the known fossil record of *Podomys*, which is limited to the Pleistocene of Florida, to test for a long-term relationship between *Podomys* and *Gopherus* (Jones and Layne, 1993). We hypothesize that in the fossil record, *Podomys* and *Gopherus* do not have a significant, long-term association, consistent with other records of species disassociations over geologic time (Owen et al., 2000). Given the asymmetric nature of the relationship between *Podomys* and *Gopherus* in the modern biota, the expectations for the presence of one species at a fossil site given the presence of the other are also asymmetric. *Podomys* benefits from the microhabitat provided by burrows of *Gopherus*, and it is most appropriate to test the longevity of the association through the presence or absence of *Gopherus* at fossils sites where *Podomys* is found. If the two species have a long-term association consistent with the preference of *Podomys* to occupy the burrows of *Gopherus*, then *Gopherus* should be present at sites where *Podomys* is found more often than expected by chance. If the current commensal relationship is a coincidental result of overlapping geographic ranges of the two species in the present day, then the 1.35 million year-long fossil record of sites containing *Podomys* should have no more occurrences of *Gopherus* than expected by chance.

Examining the reverse condition, or the presence or absence of *Podomys* at sites where *Gopherus* is found, provides additional evidence about the potential for association. In contrast to the benefit that *Gopherus* provides *Podomys*, *Podomys* provides no cost or benefit to *Gopherus*. A long-term relationship consistent with the current one should result in sites containing *Gopherus* having no more occurrences of *Podomys* than expected by chance.

MATERIALS AND METHODS

We developed a list of sites where *Podomys floridanus* is documented by searching the literature for records of the species (Bader, 1957; Pinkham, 1971; Martin, 1974; Martin and Webb, 1974; Webb, 1974; Ober, 1978; Morgan, 1991; Morgan and White, 1995; Franz and Quitmyer, 2005). In addition, we queried the Florida Museum of Natural History's Vertebrate Paleontology (FLMNH VP) online database (http://www.flmnh.ufl.edu/vertpaleo-search/) for the genus and species '*Podomys floridanus*' (accessed 14 April 2016). From each site where fossils of *Podomys* were reported, the FLMNH VP database was also queried for records of *Gopherus* (Fig. 1). The list of sites was also checked against the most recent review of the fossil record of *Gopherus* (Franz and Quitmyer, 2005). Database identifications were assumed to be correct. In the literature, teeth or mandibles of *Podomys* are diagnosed based primarily on their large size and the relative rarity or absence of accessory upper and lower molar cusps such as the mesostyle/mesostylid and ectostyle/ectostylid (Martin, 1967; Pinkham, 1971). The identification of *Gopherus* is based primarily on shell features, as reviewed in Franz and Quitmyer (Franz and Quitmyer, 2005).

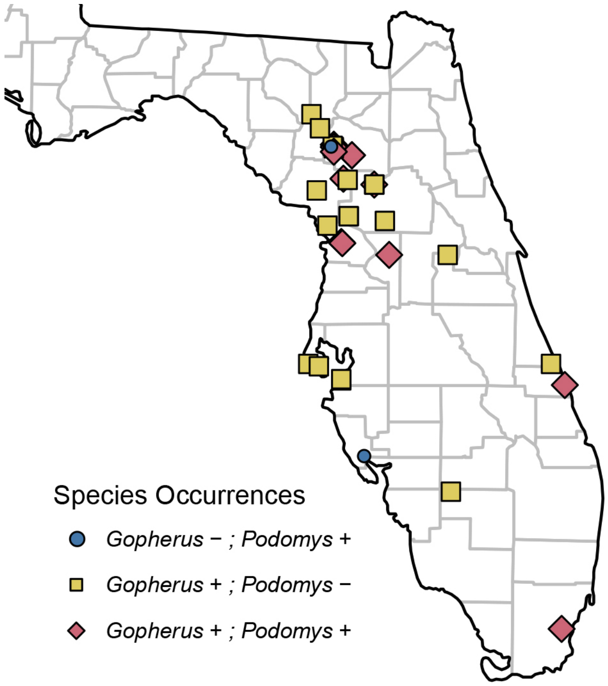

Figure 1. Map of fossil sites containing *Podomys floridanus* and *Gopherus polyphemus* among Rancholabrean and Irvingtonian faunas of Florida.

A single specimen of *Podomys* was reported from the Fort Meade Mine #7 Dragline, but we excluded this site from further analysis. The mine generally preserves fossils from the Pliocene Palmetto Fauna, but that specimen likely comes from overlying Pleistocene sands because all other fossils of *Podomys* are from Irvingtonian, Rancholabrean, or Holocene North American Land Mammal Age (NALMA) sites and other collections from the mine draglines are known to be temporally mixed (Webb et al., 2008). We also excluded he site Inglis 1A from analyses, despite reports of the presence of *Podomys* by Martin and Webb (1974), because of contrary reports in Webb (1974) and Ruez (2001).

In order to account for poorly sampled sites, we recorded the total number of specimens catalogued at each site to evaluate the possibility that fossils of *Gopherus* were present at the site but missed by chance. We excluded sites containing fewer than 50 fossils from further analyses (Forcino, 2012). In addition, we assembled faunal lists and site descriptions for localities at which *Gopherus* was not present using the FLMNH VP database to explore what might explain the absence of *Gopherus*. The FLMNH VP database contains over 37,000 records of Pleistocene small mammals and more than 560,000 records in total, and is therefore appropriate for such searches.

If a significant number of sites containing *Podomys* did not also contain *Gopherus,* we were interested to know if other burrowing animals were associated with *Podomys.* For each site, we also searched the FLMNH VP database for other taxa whose burrows *Podomys floridanus* is associated with in modern ecosystems: *Dasypus* spp., *Geomys* spp., *Peromyscus polionotus*, and *Sigmodon* spp. (Layne, 1990). Queries to the FLMNH VP database used genus names in the absence of species names to account for chronospecies as well as a range of identification precision. The exception to the practice of query-by-genus was for *Peromyscus polionotus*, because other extant species of *Peromyscus* are present in the Pleistocene fossil record of Florida. Although many species of *Peromyscus* are difficult to discriminate from each other based on isolated teeth in the fossil record, *P. polionotus* can be discriminated from other species of *Peromyscus* in the fossil record of Florida based on size, similar to *Podomys* (Pinkham, 1971).

It is not clear whether or not *Dasypus bellus* constructed burrows that could have been used by *Podomys*. However, the current hypotheses of close relationships to either (a) *Dasypus kappleri* or (b) *Dasypus novemcincus* correspond to the reconstruction of *D. bellus* as a burrower commensurate to *Dasypus novemcinctus* (Vizcaíno and Milne, 2002; Rincón et al., 2008). We therefore included records of *D. bellus* in our analyses of potential burrow associates of *Podomys*.

We constructed a second, complementary dataset by searching the FLMNH VP database for all sites containing *Gopherus* within the same spatiotemporal extent as the fossil record of *Podomys* (i.e., Irvingtonian to Rancholabrean faunas of Florida; Fig. 1). The site list was checked against the review of Franz and Quitmyer (2005) and all missing sites were added to the dataset. We also collected the total number of fossils catalogued per site and records for the same suite of taxa examined in the first analysis. In addition, it is possible that *Podomys* was present, but not collected, at a site that wasn't screenwashed. Furthermore, it is possible that specimens of *Podomys*, as a member of *Peromyscus* sensu lato (Platt et al., 2015), and *P. polionotus* were more coarsely identified as *Peromyscus* sp. at certain sites where they are present. To account for these possibilities, records for all rodents from each candidate site were collected as a proxy for screenwash effort. In those cases where small rodent teeth were not collected, it is highly unlikely that taxa such as *Podomys* would be identified even if they were present in the fauna. Those sites that did not contain any rodents, or which did not contain teeth of small rodents such as *Sigmodon*, *Geomys*, *Neotoma*, *Peromyscus*, or even indeterminate Muridae were excluded from analyses. We further searched for any records of *Peromyscus* sp. at remaining sites to examine whether identification practices could have affected our results in regards to *Podomys* and *Peromyscus polionotus*.

Chi-square tests are sometimes used to compare species occurrences to test for association with the null hypothesis that the two species are both independent of each other in locality occupation (McCulloch, 1985; Calede et al., 2011). However, in this case it is not informative to test for symmetrical independence of the two species because the alternative hypothesis under investigation addresses an asymmetrical presence-absence expectation. In the particular case of *Podomys* and

Gopherus, the independence of the presence of *Gopherus* with respect to *Podomys* might result in a failure to reject the null hypothesis using a chi-square test, but that result would be uninformative about the potential non-independence of *Podomys* with respect to *Gopherus*. Instead, exact, one-tailed binomial tests were used to evaluate the probability of significant species-pair associations at a greater frequency than the null hypothesis. The null hypothesis of no significant association was modelled with a probability of success of 0.5. For each dataset, the p-values of the five tests were classically Bonferroni corrected by dividing original p-values by the number of tests and accepting as significant those transformed values that remained less than an alpha of 0.05 (Holm, 1979). Data were organized and analyzed in R 3.2.4 (R Core Team, 2015).

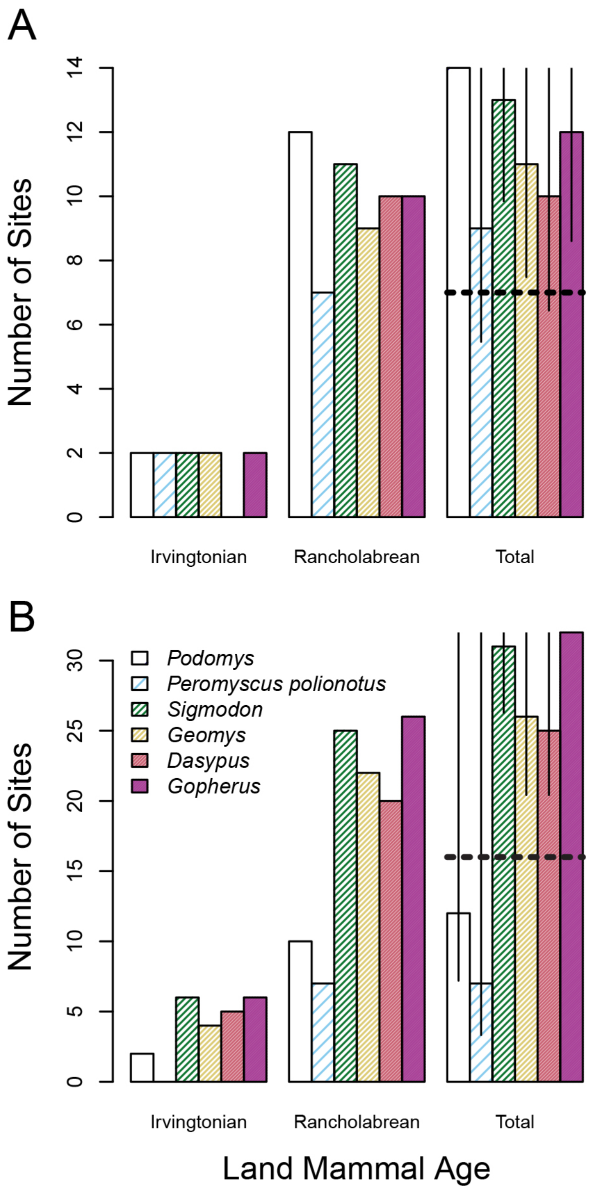

Figure 2. Counts of burrowing taxon occurrences at **A**. fourteen fossil sites in Florida containing *Podomys floridanus* or **B**. thirty-three fossil sites from the same spatial and biostratigraphic extent that contain *Gopherus polyphemus*. Sites are first discriminated by North American Land Mammal Age (left), then combined to show total site counts (right). Thin, black lines on bars indicate confidence intervals for one-tailed binomial tests. Thick, dashed black lines indicate the number of sites expected according to the null hypothesis (species present at 50% of sites that preserve a given species of interest).

RESULTS

Podomys floridanus is known from a total of 17 sites, containing Irvingtonian to Rancholabrean faunas. Based on the estimated age of those faunas, the fossil record of *P. floridanus* spans ~1.35 Ma – 0.01 Ma (Bell et al., 2004). Of those sites, three (Arredondo 2C, Haile 13B, Haile 14B) were excluded because of low total sample sizes.

Of the remaining 14 sites, *Gopherus* was present at 12 (86%, Fig. 2A, Table 1), significantly more than would be expected by chance (p = 0.032). The 14 sites span the Irvingtonian and Rancholabrean NALMA. The two remaining sites where *Podomys* was present but *Gopherus* was absent were both Rancholabrean and contained other burrowing vertebrates. At Warm Mineral Springs, *Peromyscus polionotus* and *Sigmodon hispidus* were recovered. At Haile 11B, *Dasypus bellus*, *Geomys pinetis*, *P. polionotus*, and *S. hispidus* were all present. Of the other burrowing taxa with which *Podomys* is known to associate, only *S. hispidus* had a significantly strong association with *Podomys* (p = 0.005, Fig. 2A).

Based on a second database and literature search, *Gopherus* was present at 67 sites in the same spatiotemporal extent as the fossil record of *Podomys*. Of those 67 sites, 23 were removed for

TABLE 1. Florida fossil sites containing *Podomys floridanus* that meet minimum criteria of fossil abundance and presence of turtles (see Materials & Methods for justification), as well as records of reported burrow associates. Abbreviations: n = total number of specimens catalogued from the site.

Site	n	*Podomys*	*Gopherus*	*Dasypus*	*Geomys*	*P. polionotus*	*Sigmodon*	Land Mammal Age
Arredondo 1A	372	+	+	+	+		+	Rancholabrean
Arredondo 2A	692	+	+	+	+	+	+	Rancholabrean
Coleman 2A	949	+	+	+	+		+	Irvingtonian
Devil's Den	3410	+	+	+	+	+	+	Rancholabrean
Haile 11A	73	+	+		+	+	+	Rancholabrean
Haile 11B	1335	+		+	+	+	+	Rancholabrean
Haile 21A	2019	+	+	+				Irvingtonian
Lecanto 2A	2131	+	+	+	+		+	Rancholabrean
Monkey Jungle Hammock	1021	+	+	+			+	Rancholabrean
Reddick 1A	10449	+	+	+	+	+	+	Rancholabrean
Sabertooth Cave	1169	+	+		+	+	+	Rancholabrean
Surprise Cave	2281	+	+		+	+	+	Rancholabrean
Vero	1694	+	+	+	+	+	+	Rancholabrean
Warm Mineral Springs	263	+				+	+	Rancholabrean

having low sample sizes. An additional 11 sites were removed based on an absence of fossilized teeth of small rodents, which would preclude the identification of taxa such as *Podomys*. Of the remaining 33 sites containing fossils of *Gopherus*, *Podomys* was only recovered in the same 12 sites discussed above, or 36% of the sites (Table 1). Of the five other mammalian taxa studied, three (*Dasypus*, *Geomys*, and *Sigmodon*) had a significant association with *Gopherus* ($p = 0.003$, 0.003, <0.000001, respectively, Fig. 2B).

Peromyscus sp., but not *Podomys floridanus* or *Peromyscus polionotus*, was found at four of the 33 candidate sites (Haile 8A, Haile 13A, Haile 14A, and Reddick 1C). It is possible that fossils of *P. polionotus* and *Podomys*, as members of *Peromyscus* sensu lato, may not have been identified to the species level in these four sites. However, even if those collections of *Peromyscus* sp. were to contain fossils of both *Podomys* and *P. polionotus*, then the two taxa would still be present in fewer than 50% of the candidate sites containing *Gopherus* (16 and 11 sites, 48% and 33%, respectively).

DISCUSSION

Throughout the known fossil record of *Podomys*, the species has a significant association with *Gopherus*. *Podomys* also has a close association with *Sigmodon* spp. throughout the same interval. Both *Podomys* and *Sigmodon* are known to inhabit burrows of *Gopherus* (Lips, 1991; Witz et al., 1991). Although co-occurrence at the same site does not demonstrate a commensal relationship between any pair of these species, it is consistent with such a hypothesis. A reciprocal, close association of *Podomys* in the fossil record of *Gopherus* was not found in our study (Fig. 2B). That lack of association is also consistent with a commensal relationship in which individuals of *Podomys* benefits from the presence of *Gopherus* burrows, but individuals of *Gopherus* are unaffected by the presence or absence of *Podomys*.

Division of the faunas into Rancholabrean (160-10 ka; Bell et al., 2004) and Irvingtonian (1,350-160 ka; Bell et al., 2004) NALMAs support the hypothesis that the association between the two taxa is not limited to a single portion of the fossil record of *Podomys*, but is present throughout. In addition, the presence of other burrowing species, specifically *Geomys pinetis*, *Peromyscus polionotus*, and *Sigmodon hispidus*, and likely the extinct *Dasypus bellus* (Vizcaíno and Milne, 2002; Rincón et al., 2008), at the same fossil sites as *Podomys* supports the hypothesis that individuals of *Podomys* need not have dug their own burrows since the Irvingtonian.

The two sites containing *Podomys* but lacking *Gopherus* are not taphonomically remarkable in comparison to other fossil sites from the fissure fills and sinkholes of other springs and the Haile quarry (Clausen et al., 1975; Morgan and Emslie, 2010). Based on the faunal lists assembled, both sites contain fossils of the terrestrial, giant tortoise *Hesperotestudo* as well as other terrestrial mammals. It is not known if *Hesperotestudo* burrowed like *Gopherus*. There is no *a priori* reason to expect *Gopherus* to be absent from either site.

Alternative hypotheses could be proposed to explain the co-occurrence patterns found in this study. The co-occurrence of *Podomys*, *Peromyscus polionotus*, and *Geomys* together was previously proposed to be a proxy for a xeric environment (Franz and Quitmyer, 2005). In the modern biota, those three taxa are restricted to well-drained soils (Gentry and Smith, 1968; Wilkins, 1987; Franz and Quitmyer, 2005). It is possible that *Geomys*, *P. polionotus*, and *Gopherus* are frequently found at sites with *Podomys* because they all inhabited the same xeric habitat and not because any taxon was inhabiting the burrows of any other taxon. The two hypotheses, species interaction and habitat similarity, are not mutually exclusive and mirror present-day conditions for those species (Jones and Layne, 1993). The two hypotheses would only be separable in the fossil record if both *Podomys* and one of the other candidate species were found together at a site that was demonstrably not derived from a xeric habitat. Such a situation would indicate that the habitat tolerances had changed over time (Findley, 1964; Davis et al. 2014). If all four taxa had habitat restrictions in the past similar to their current habitat restrictions, then we expect to see a large number of sites that preserve *Gopherus*, *Geomys*, and *P. polionotus* given the presence *Podomys*. The lack of significant association of *Geomys* and *P. polionotus* with *Podomys* in the fossil record after p-values are corrected for multiple tests (Fig. 2A) is evidence against the habitat similarity hypothesis. Although the fossil record of *Gopherus* in Florida extends as far back as the hypothesized origin of the local, xeric scrub habitat in the late Pliocene or early Pleistocene (Myers, 1990; Franz and Quitmyer, 2005), the published fossil record of *Podomys*, including *Podomys* nov. sp. or *Podomys* sp., is notably shorter (Morgan and White, 1995; Ruez, 2001).

The expectation for the reverse condition, the presence or absence of other xeric taxa given the presence of *Gopherus*, may not be as informative for predictions about *Podomys*. In the modern biota, *Geomys* and *Gopherus* are found in a wider range of habitats than *Podomys* (Wilkins, 1987; Endries et al., 2009), and they might therefore be more likely to be preserved at a wider range of sites. The result of a significant association of *Geomys*, but not *Podomys*, with the presence of *Gopherus* may reflect those differences in habitats.

An additional hypothesis is that *Podomys floridanus* and *Peromyscus polionotus* are found at relatively fewer sites than other taxa because of differences in identification. That is, they were searched for in the database at the species level while other taxa were searched for at the generic level. When additional records of *Peromyscus* spp. are provisionally added to the counts of either species, in order to account for this potential bias, the two species are still not significantly associated with occurrences of *Gopherus*.

In short, the evidence supports the hypothesis that (1) *Podomys* has been associated with burrows of *Gopherus* since the early Pleistocene, or (2) *Podomys* occupied a xeric habitat even more restricted than that occupied by other taxa such as *Geomys* and *Gopherus*, or (3) some combination of both of the previous two hypotheses. All three scenarios support the hypothesis that *Podomys* evolved from an ancestor that migrated from arid regions of Mexico and the southwestern United States during the late Miocene or Pliocene (Williams et al., 1985; Platt et al., 2015).

An improved understanding of the paleontological history of species associations can help inform conservation management strategies (Willis and Birks, 2006; Hadly and Barnosky, 2009; Seddon et al., 2014). On one hand, uncovering broader association patterns that are less strict than they appear in the modern biota can open up management strategies that are not apparent from studying living animals alone (Owen et al., 2000; Hadly and Barnosky, 2009). On the other hand, documenting long-term species associations that extend through periods of abiotic change can highlight the evolutionary and ecological importance of those specific relationships and lend weight to certain conservation priorities (Willis et al., 2010). In the case documented here, evidence from the fossil record supports the hypothesis that a close association between *Podomys floridanus* and *Gopherus polyphemus* is part of the baseline ecological state of Floridian scrub and sandhill communities since the early Pleistocene.

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