Paleobiogeographic Changes at the Pleistocene–Holocene Boundary near Pintwater Cave, Southern Nevada

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In 1996, approximately 70,000 mammal and lizard bones were recovered from Pintwater Cave in the northern Mojave Desert of southern Nevada. These bones date between 32,000 and 7350 ^{14}C yr B.P. Between 32,000 and 10,100 ^{14}C yr B.P. the local fauna consisted of a mix of xeric- and cool/mesic-adapted species. *Ochotona princeps* and *Thomomys talpoides* then occupied the region, although these animals were extirpated by the onset of the middle Holocene. *Sauromalus obesus* and *Dipodomys deserti* probably migrated to the region during the latest Pleistocene. *Dipsosaurus dorsalis* entered the Pintwater Cave record after 8000 ^{14}C yr B.P. Consistent with climatic interpretations for the northern Great Basin, these data suggest a cool and moist latest Pleistocene climate for the northern Mojave Desert. In contrast to the northern Great Basin, however, this region experienced predictable summer precipitation coupled with increasingly warmer winters by 10,100 ^{14}C yr B.P. In both regions, the warm middle Holocene began ca. 8300 ^{14}C yr B.P. However, whereas the northern Great Basin probably experienced warm and dry conditions at that time, the northern Mojave Desert remained warm with relatively predictable summer precipitation. The modern northern Mojave Desert biota probably was not established until after 8300 ^{14}C yr B.P. © 2000 University of Washington.

Key Words: paleobiogeography; Pleistocene; mammals; lizards; Mojave Desert.

INTRODUCTION

Studies have been made of climate histories in the northern Mojave and Great Basin deserts for more than 50 yr. Recent contributions include Rhode and Madsen (1995) and Spaulding (1995) on plant macrofossils, Quade *et al.* (1998) on paleohydrology, and Grayson (in press) on paleobiogeography. These studies suggest that the northern Great Basin and Mojave deserts generally experienced much cooler and overall wetter climate than now before ca. 11,000 ^{14}C yr B.P. Spaulding (1995) and Quade *et al.* (1998) present evidence for increased spring recharge in the Las Vegas Valley and high stands of Pluvial Lake Mojave after 18,000 ^{14}C yr B.P. They suggest that the rising of the regional water table at this time probably was due to increased winter precipitation rather than to increased summer monsoonal flow.

The timing of the onset of the present summer monsoonal regime in the northern Mojave Desert and southern Great Basin and the possible extention of these summer rains into the northern Great Basin during the early and middle Holocene are unclear. Thompson *et al.* (1993) argued that the Great Basin experienced increased summer monsoonal flow during the early Holocene, whereas Grayson (in press) recently argued that the northern Great Basin was cool and wet during this time, rather than warm and wet. Grayson's (in press) paleobiogeographic work at Homestead Cave also indicates that a warm, dry period began ca. 8300 ^{14}C yr B.P. following the relatively wet and cool early Holocene.

Recent excavations in Pintwater Cave in the northern Mojave Desert retrieved a rich and diverse faunal assemblage consisting of approximately 70,000 specimens spanning the late Pleistocene to middle Holocene. These bones provide information about the cool and wet Pleistocene climate of the northern Mojave Desert, the onset of summer monsoonal rains in the region before the end of the Pleistocene, and the onset of the warm middle Holocene climate.

Although several studies have been published about Pleistocene and early Holocene faunal assemblages recovered from the northern Mojave Desert, these assemblages are from individual woodrat middens (e.g., Mehringer and Ferguson, 1969; Mead and Spaulding, 1995), from cave sites lacking stratigraphic control or multiple radiocarbon dates (e.g., Reynolds *et al.,* 1991), or from open-air contexts (e.g., Quade *et al.,* 1998). The Pintwater Cave faunal assemblage is the first sample from the northern Mojave Desert to be recovered from an undisturbed cave matrix with multiple radiocarbon dates.

PINTWATER CAVE

Pintwater Cave is located in the southern Pintwater Range in the northern Mojave Desert of southern Nevada at 1268 m altitude (Fig. 1). Vegetation growing within several hundred meters of the cave is typical of a Mojave Desert scrub community: *Ambrosia dumosa* (white bursage), *Larrea tridentata* (creoste bush), *Atriplex confertifolia* (shadscale), *Ephedra nevadensis* (Mormon tea), *Stipa speciosa* (desert needle grass), *Yucca schidigera* (Mojave yucca), and *Ferocactus acanthodes*
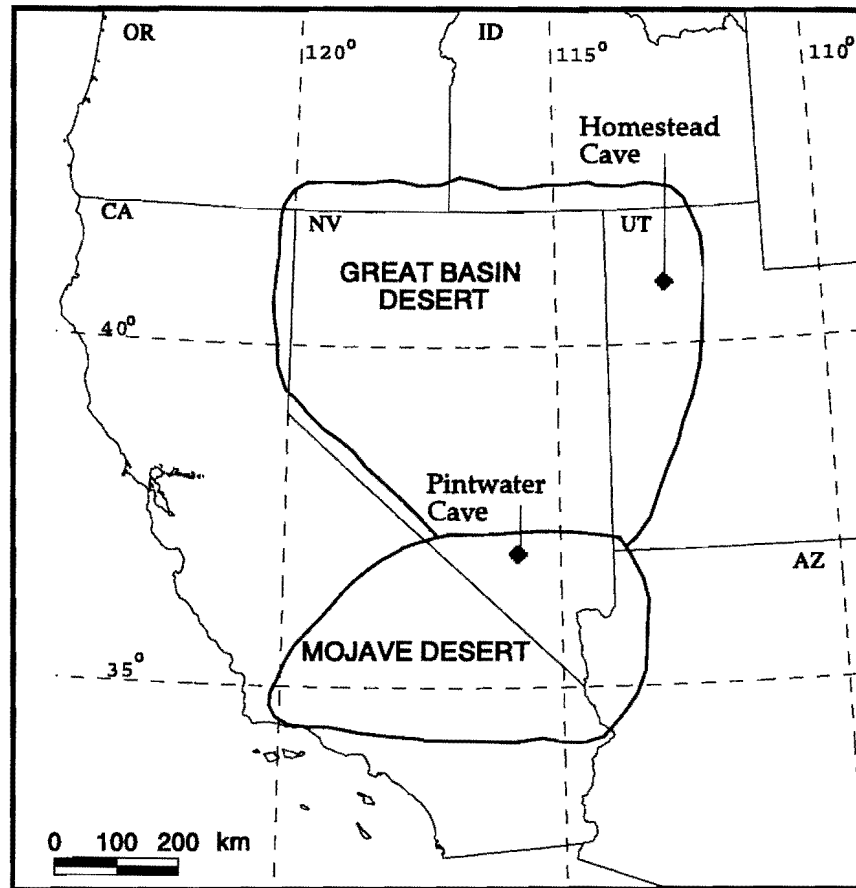
FIG. 1. Map of the American Southwest showing locations of Pintwater and Homestead caves and the general outlines of the Mojave and Great Basin deserts.

(California barrel cactus). Trees, found only in the extreme northern portion of the Pintwater Range, are mainly scattered *Pinus monophylla* (pinyon pine) and *Juniperus osteosperma* (Utah juniper) (Buck, 1997).

Five test units were excavated in Pintwater Cave in 1996. The faunal remains recovered from Unit 3 are reported here because approximately 80% of the 70,000 bones recovered were found within this unit. Most of the bones in Unit 3 were from degraded owl pellets, whereas most of the remainder were deposited in carnivore scats. These interpretations are based on the following observations: (1) the assemblage consists mainly of complete or nearly complete rodent and leporid bones (Dodson and Wexlar, 1979); (2) many bones display slight polishing and minimal corrosive damage caused by digestive enzymes, as opposed to the high degree of corrosive damage seen in bones deposited in carnivore scats (Andrews and Evans, 1983) and in diurnal raptor pellets (Hockett, 1996); (3) many bones have pellet or scat material adhering to notches and cavities; (4) several bones exhibit puncture marks created by raptor beaks or talons, or by carnivore teeth (Hockett, 1991, 1999); (5) several bones display shearing damage characteristic

of raptor-accumulated assemblages (Guilday and Parmalee, 1965); and (6) none of the bones, including the unidentifiable bone fragments, was burned.

Unit 3 was situated beneath a ledge repeatedly used by roosting owls between the late Pleistocene and middle Holocene. As a result, much of the sediment in Unit 3 consists almost entirely of degraded raptor pellets mixed with lesser amounts of silt, roof spalls, and mountain sheep (*Ovis canadensis*) dung. The top 5 cm of the unit consists of loose, fine silt (stratum 1). The degraded pellets (stratum 2) did not form internally recognizable lenses, although the unit was only excavated to a depth of 75 cm. Bedrock was estimated to lie several meters below the base of the excavated unit; therefore, the degraded raptor pellet debris probably represents an upper stratum separated by deeper, unexcavated strata below.

Because stratum 2 was at least 65 cm thick, it was sampled by excavating arbitrarily at 10-cm levels to gain more precise vertical and temporal control within the stratum (Fig. 2). Radiocarbon dates were obtained from six of the eight levels excavated within Unit 3 (Buck, 1997; Fig. 2 and Table 1), producing a chronologically ordered suite of dates.
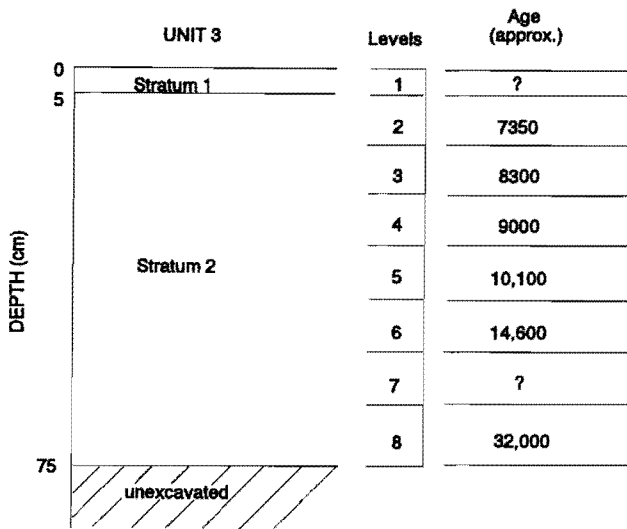
FIG. 2. Diagram showing relationships and ages of strata and levels excavated in Unit 3, Pintwater Cave.

GENERAL SPECIES ACCOUNTS

Nineteen genera and species of mammals and six genera and species of lizards were identified from Unit 3 (Table 2). Most of the potentially identifiable bones recovered in Unit 3 consist of postcranial remains of small rodents. Therefore, a sampling strategy was devised before the bones were identified (Appendix I).

A number of extant mammals and lizards have been present in the northern Mojave Desert for at least the past 15,000 yr, e.g., *Microtus* sp. (vole), *Neotoma cinerea* (bushy-tailed woodrat), *Neotoma lepida* (desert woodrat), *Thomomys bottae* (southern pocket gopher), *Ovis canadensis* (mountain sheep), *Antrozous pallidus* (pallid bat), *Crotaphytus collaris* (collared lizard), and *Gambelia wislezini* (leopard lizard).

Previous faunal records have established the presence of pika (*Ochotona princeps*) and marmot (*Marmota flaviventris*), as well as a host of extinct megafauna in the Pleistocene Mojave Desert (e.g., Mawby, 1967; Jefferson, 1982). Pintwater Cave provides the first late Pleistocene paleontological record of the northern pocket gopher (*Thomomys talpoides*) from the region. *Mustela* cf. *erminea* (short-tailed weasel) and *Canis lupus* (gray wolf) were also present in the late Pleistocene deposits of Pintwater Cave, providing the first Pleistocene regional record of the wolf. Spaulding (1995) noted a general lack of large carnivores in the Pleistocene fauna of the northern Mojave Desert. The lack of large carnivores or any form of extinct megafauna in Pintwater Cave is not surprising, given the limited excavation which has occurred in the cave and the fact that a majority of the bones recovered were obtained from degraded raptor pellets and carnivore scats. The largest animal identified from the cave remains was *Ovis canadensis*. Mountain sheep bones and dung were found in the lowest level of Unit 3, dated to ca. 32,000 ^{14}C yr B.P.

ACCOUNTS OF SELECTED SPECIES

Ochotona princeps

Pika mandibles were recovered in levels 2, 4, and 5, which date to ca. 7350, 9000, and 10,100 ^{14}C yr B.P., respectively. It is unlikely that the mandibles were brought to the site from beyond the Mojave Desert by raptors because predatory birds rarely kill pika in the Americas (Smith and Weston, 1990). In addition, pika dung pellets have been dated to 47,000 ^{14}C yr B.P. in the northern Mojave Desert, and Pleistocene pika remains have been found only 16 km east of Pintwater Cave in the Sheep Range, and 32 km southwest of the cave in the Spring Range (Mead and Spaulding, 1995). Holocene pika remains have been found above a level dated at 9830 ^{14}C yr B.P. in Kokoweef Cave south of Pintwater Cave (Reynolds *et al.*, 1991).

Mead and Spaulding (1995) argued that pika may have been extirpated from the valley floor localities of the northern Mojave Desert by 14,000 ^{14}C yr B.P. All pika mandibles recovered from Pintwater Cave date to the early Holocene and the latest Pleistocene, but this may not mean that these animals were present along valley floors after 14,000 ^{14}C yr B.P. Pika may have occupied only the higher elevations of mountains (e.g., Spring or Sheep ranges) at this time, and were subsequently deposited in the lower-elevation Pintwater Cave by raptors. Nevertheless, the pika from Pintwater Cave are evidence of the early Holocene presence of this species in the northern Mojave Desert.

Thomomys talpoides

Thomomys talpoides occurred in levels 4, 6, 7, and 8 of Unit 3, or approximately between 32,000 and 9000 ^{14}C yr B.P. The northern pocket gopher now lives at least 240 km north of Pintwater Cave in central and northern Nevada (Hall, 1946), where it requires relatively cool, mesic conditions for survival. The cooler climate of the late Pleistocene allowed *T. talpoides* to occupy the northern Mojave Desert, together with *T. bottae*

TABLE 1

Chronological Ordering of the Eight Levels Excavated in Unit 3, Pintwater Cave (after Buck, 1997)

Excavation level	Age (^{14}C yr B.P.)	Desert Research Institute lab No.
1	not dated	
2	7349 ± 64	DRI-3082
3	8312 ± 130	DRI-3136
4	9042 ± 72	DRI-3081
5	10,063 ± 90	DRI-3137
6	14,684 ± 190	DRI-3138
7	not dated	
8	31,899 ± 473	DRI-3084

Note. All dates were obtained from *Ovis canadensis* dung pellets.

TABLE 2
Number of Identified Specimens of Mammalian and Lizard Genera and Species from Unit 3, Pintwater Cave

Taxa	Excavation level								Totals
	1	2	3	4	5	6	7	8	
Leporidae									
Lepus cf. californicus	16	84	74	139	61	35	42	28	479
Sylvilagus spp.		8	2	1	4		11	1	27
Ochotonidae									
Ochotona princeps[a]		1		1	2				4
Muridae									
Microtus sp.	2	7	4	20	16	14	21	19	103
Neotoma cinerea			1	3	4	2	1	4	15
Neotoma lepida	5	7	10	38	34	27	24	18	163
Onychomys spp.					1				1
Peromyscus spp.		1				1	1	2	5
Sciuridae									
Ammospermophilus leucurus	1	6	2	10	10	10	6	12	57
Geomyidae									
Thomomys bottae	8	9	3	15	31	37	43	52	198
Thomomys talpoides[a]				3		1	6	1	11
Heteromyidae									
Dipodomys deserti	6	16	6	7	1				36
Dipodomys merriami		1	2						3
Dipodomys microps			3	1	1				5
Dipodomys panamintinus		1					1	1	3
Perognathus spp.			1	1					2
Mustelidae									
Mustela erminea[a]					1				1
Canidae									
Canis latrans								1	1
Canis lupus[a]								1	1
Felidae									
Lynx rufus		1		1					2
Bovidae									
Ovis canadensis	3	3	1	4	2		2	1	16
Vespertilionidae									
Antrozous pallidus		9		7	12	15	10	7	60
Iguanidae									
Crotaphytus collaris	1	3	5	3	15	13	4	4	48
Dipsosaurus dorsalis		3							3
Gambelia wislezini	1	5	1	4	20	13	12	11	66
Phrynosoma platyrhinos	1		1	2	1		2	1	8
Sauromalus obesus	9	39	10	3	4				65
Teiidae									
Cnemidophorus sp.		1	4			1			6

[a] Species does not inhabit northern Mojave Desert today.

(southern pocket gopher). Based on the Pintwater faunal record, *T. talpoides* was extirpated from the region by the beginning of the middle Holocene, ca. 8300 ¹⁴C yr B.P.

Dipodomys deserti

The desert kangaroo rat currently occupies nearly all of Clark County in southern Nevada (Hall, 1946). *Dipodomys deserti* may have entered the northern Mojave Desert ca.

10,100 ¹⁴C yr B.P. Of the 36 *D. deserti* mandibles identified from Pintwater Cave, however, 35 dated between 9000 and 7350 ¹⁴C yr B.P.

The desert kangaroo rat is the most specialized of all the species of *Dipodomys* (Best *et al.*, 1989) and is now found in the Lower Sonoran Life Zone and the lowest and hottest areas of the Upper Sonoran Life Zone (Hall, 1946). Throughout its range, *D. deserti* is only found in relatively high sand dunes (Best *et al.*, 1989; Hall, 1946).

Herpetofauna

Crotaphtus collaris, Gambelia wislezini, Cnemidophorus sp. (whiptail), and *Phrynosoma platyrhinos* (desert horned lizard) probably have been present near Pintwater Cave for the past 32,000 yr. *Sauromalus obesus* (chuckwalla) entered the Pintwater Cave faunal record about 10,100 ^{14}C yr B.P., and *Dipsosaurus dorsalis* (desert iguana) entered the faunal record during the middle Holocene, about 7350 ^{14}C yr B.P.

The chuckwalla occupies the Lower Sonoran Life Zone in the Sonoran and Mojave deserts. The Mojave Desert represents the northern limit of habitat tolerance for the chuckwalla. Chuckwalla reach maximum levels of reproductive success in areas of mild winter temperature and predictable summer rainfall (Abts, 1987). Southern populations of chuckwalla, which inhabit the Sonoran Desert, have year-round activity and high levels of reproductive success, while northern populations in much of the Mojave Desert have perhaps one-quarter of the reproductive success rate of their Sonoran Desert counterparts (Abts, 1987). The desert iguana is also restricted to the Lower Sonoran Life Zone, usually in open, sandy areas (Norris, 1953). The desert iguana may be the most heat-tolerant species of all the North American lizards. In its northern Mojave Desert range, the desert iguana must hibernate six months of the year (October–March) (Norris, 1953).

Previous studies have noted that late Pleistocene herpetofaunas from the Mojave Desert are characterized by (1) their modern taxonomic character (Norell, 1986), (2) cool, mesic-adapted mammalian fauna living in sympatry with a "xeric" lizard fauna (Norell, 1986), (3) the presence of the chuckwalla and leopard lizard in habitats other than desert scrub (pinyon-juniper or juniper woodlands), thus the restriction of these taxa to desert scrub is a relatively recent phenomena (Van Devender and Mead, 1978), and (4) the presence of chuckwalla in the late Pleistocene faunal record but the absence of the desert iguana in the late Pleistocene and early Holocene records (Brattstrom, 1954; Van Devender and Mead, 1978; Norell, 1986). The herpetofauna from Pintwater Cave, in general, corroborates these interpretations.

DISCUSSION AND CONCLUSION

Unit 3 in Pintwater Cave records significant paleobiogeographic changes between 32,000 and 7350 ^{14}C yr B.P. in the northern Mojave Desert. The well-dated paleofaunal cave record and the climatic implications of these data corroborate some previous interpretations of climatic histories in the northern Mojave and Great Basin deserts, but contrast with others.

The presence of *O. princeps* and *T. talpoides*, the abundance of *Microtus* specimens, and the absence of warm-adapted species such as *D. deserti, Sauromalus obesus,* and *Dipsosaurus dorsalis* in the Pleistocene deposits of the cave all suggest a cool and wet climate for the northern Mojave Desert before 10,100 ^{14}C yr B.P. These data are consistent with paleovegeta-

tion records, pluvial lake cycles, and paleohydrologic studies for the region (Woodcock, 1986; Spaulding, 1995; Quade *et al.,* 1998). Barring a lengthy lag time for the migration of the chuckwalla from its presumed full-glacial homeland to the south, the absence of this lizard until the latest Pleistocene is consistent with the predominantly winter precipitation model for the northern Mojave Desert during late-glacial through Younger Dryas time, or from approximately 18,000 to 10,500 ^{14}C yr B.P.

Based on the 10,100 ^{14}C yr B.P. date for the earliest chuckwalla remains in Pintwater Cave, the switch from predominantly winter precipitation to a more summer monsoonal flow likely occurred between 11,000 and 10,100 ^{14}C yr B.P., which accords with Woodcock's (1986) paleovegetation study from the Death Valley region. A relatively warm latest Pleistocene climate, coupled with increased sand dune activity, is indicated by the presence of the desert kangaroo rat in the Pintwater record between approximately 10,100 and 9000 ^{14}C yr B.P.

Both the northern Great Basin and the northern Mojave Desert seem to show a nearly synchronous onset of the relatively warm temperatures of the middle Holocene ca. 8300 ^{14}C yr B.P. At Homestead Cave in the northern Great Basin, *Microtus* numbers fell dramatically and *Marmota flaviventris* and *Brachylagus idahoensis* (pygmy rabbit) became locally extinct ca. 8300 ^{14}C yr B.P. At Pintwater Cave, *Microtus* numbers also decrease dramatically and *T. talpoides* became locally extinct ca. 8300 ^{14}C yr B.P. However, while the northern Great Basin was warm and dry during the middle Holocene, the Pintwater Cave data suggest a continuation of monsoonal rains in the northern Mojave Desert, as the remains of chuckwalla become increasingly abundant beginning 8300 ^{14}C yr B.P. and remain abundant at ca. 7350 ^{14}C yr B.P. Spaulding (1991a), however, argues for relative aridity in the northern Mojave Desert by 6800 ^{14}C yr B.P.

The changeover from a Pleistocene to a more modern ecosystem did not occur in the northern Mojave and Great Basin deserts until the middle Holocene (Grayson, 1987, in press; Rhode and Madsen, 1995; Spaulding, 1995), and the Pintwater Cave data corroborate this interpretation. In addition, the habitat requirements of modern mammal species may not always be appropriate analogues for their pre-middle Holocene distributions. Chuckwalla, for example, is closely associated with rocky habitat and creosote vegetation in the northern Mojave Desert, yet this lizard migrated into the Pintwater region ca. 10,100 ^{14}C yr B.P., perhaps 3000 yr before the establishment of creosote in the region (Spaulding, 1990, 1991b, 1995).

APPENDIX I

The sampling strategy was designed to maximize the identification of mammal and lizard species, given their primary mode of deposition in raptor pellets. Rodent, bat, and lizard mandibles and maxillae were separated for identification because raptors usually swallow the head of small prey, along

with the postcranial elements (Dodson and Wexlar, 1979). All cranial and postcranial remains of leporids, carnivores, and ungulates were separated for identification.

Mammal bones were compared to specimens housed at the Page and Los Angeles County museums; the lizard bones were compared to specimens housed at the San Bernardino County Museum. *Thomomys talpoides* was distinguished from *Thomomys bottae* based on the size and shape of the enamel plates of the premolars (Thaeler, 1980) and alveolar lengths of the mandibles (Grayson, 1985). *Dipodomys deserti* was distinguished from other species of the genus based on the size and shape of the lower premolar (Wood, 1935) and the thickness of the enamel on the lower cheek teeth. The remaining species of *Dipodomys* were identified from unique characters in the shape of the lower premolar or incisor (Wood, 1935; Csuti, 1979). *Ovis canadensis* bones are easily distinguished from other North American artiodactyls with appropriate comparative collections (Ford, 1990). *Neotoma cinerea* was distinguished from *Neotoma lepida* based on alveolar length and on the reentrant angle of the anterior prism of the lower first molar (Grayson, 1985). The *Canis lupus* specimen was a patella; its identification was based on the size and shape of multiple comparative specimens of *C. lupus*, *C. latrans*, and *C. dirus* housed at the Page Museum. The various species of *Microtus* that inhabit western North America may be indistinguishable based on dental characters (Grayson, 1983); thus, no species designation is offered here. In *Sauromalus*, the lower posterior teeth possess five lobes, whereas the anterior teeth possess three lobes; in *Dipsosaurus*, the mandibular teeth and all the upper teeth on the maxilla are tricuspidate (Cope, 1900). *Crotaphytus collaris* is distinguishable from *Gambelia wislezini* in possessing less-curved mandibular teeth and a more-rounded, less-sharply angled anterior mandible. *Cnemidophorus* is distinguished by a thin, straight, and anteriorly pointed mandible. *Antrozous pallidus* is distinguished by a unique dental formula and a high coronoid process on the dentary.

ACKNOWLEDGMENTS

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