Helodermatid Lizard from the Mio-Pliocene Oak-Hickory Forest of Tennessee, Eastern USA, and a Review of Monstersaurian Osteoderms

Authors: Mead, Jim I., Schubert, Blaine W., Wallace, Steven C., and Swift, Sandra L.

Source: Acta Palaeontologica Polonica, 57(1) : 111-121

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2010.0083

Helodermatid lizard from the Mio-Pliocene oak-hickory forest of Tennessee, eastern USA, and a review of monstersaurian osteoderms

JIM I. MEAD, BLAINE W. SCHUBERT, STEVEN C. WALLACE, and SANDRA L. SWIFT

Mead, J.I., Schubert, B.W., Wallace, S.C., and Swift, S.L. 2012. Helodermatid lizard from the Mio-Pliocene oak-hickory forest of Tennessee, eastern USA, and a review of monstersaurian osteoderms. *Acta Palaeontologica Polonica* 57 (1): 111–121.

The extant venomous Gila monster and beaded lizards, species of *Heloderma*, live today in southwestern USA and south along the Pacific coastal region into Central America, but their fossil history is poorly understood. Here we report helodermatid osteoderms (dermal ossicles) from the late Miocene–early Pliocene Gray Fossil Site, eastern Tennessee USA. Twenty-three species of mammals are known from the fauna including abundant *Tapirus polkensis*, as well as fishes, anurans, salamanders, turtles, *Alligator*, birds, and snakes. Beaded lizards belong to the Monstersauria, a clade that includes *Primaderma* + *Paraderma* + *Gobiderma* + Helodermatidae (*Estesia, Eurheloderma*, *Lowesaurus*, and *Heloderma*). Osteoderms of lizards in this clade are unique within Squamata; they typically are circular to polygonal in outline, domed to flat-domed in cross-section, have a vermiculate surface texture, are not compound structures, and do not have imbricate surfaces as on many scincomorph and anguid lizards. We review and characterize the osteoderms of all members of Monstersauria. Osteoderms from the cranium, body, and limbs of *Heloderma* characteristically have a ring-extension (bony flange) at least partly surrounding the dome. Its presence appears to be a key character distinct to all species of *Heloderma*, consequently, we propose the presence of a ring-extension to be an apomorphy. Three osteoderms from the Gray Fossil Site range from 1.5 to 3.0 mm in diameter, have the circular shape of helodermatid osteoderms with a domed apical surface, and have the ring-extensions, permiting generic identification. Macrobotanical remains from the Gray Fossil Site indicate an oak-hickory subtropical forest dominated by *Quercus* (oak) and *Carya* (hickory) with some conifer species, an understorey including the climbing vines *Sinomenium*, *Sargentodoxa*, and *Vitis*. Plant and mammal remains indicate a strong Asian influence.

Key words: Reptilia, Squamata, Helodermatidae, *Heloderma*, beaded lizards, Hemphillian, Miocene, Pliocene, Tennessee, North America.

Jim I. Mead [mead@etsu.edu], Blaine W. Schubert [schubert@etsu.edu], Steven C. Wallace [wallaces@etsu.edu], and Sandra L. Swift [Sandra.swiftone@yahoo.com], Department of Geosciences, and the Don Sundquist Center of Excellence in Paleontology, East Tennessee State University, Johnson City, TN 37614 USA.

Received 25 August 2010, accepted 11 March 2011, available online 14 March 2011.

Introduction

The only truly venomous lizards today are the Gila monster and beaded lizard, both in the genus *Heloderma* (Wiegmann 1829), in the Family Helodermatidae. These large lizards live in southwestern USA and south along the Pacific coastal region into Central America. Their fossil history is inadequately understood as it is for all members of the Monstersauria, a clade including *Primaderma* + *Paraderma* + *Gobiderma* + Helodermatidae (*Estesia, Eurheloderma, Lowesaurus*, and *Heloderma*) (Norell and Gao 1997), as discussed and illustrated in Conrad (2008: fig. 56D; see further discussions in McDowell and Bogert 1954; Bogert and Martín del Campo 1956; Pregill et al. 1986). Here we report helodermatid osteoderms (dermal ossicles) from the late Miocene–early Pliocene of the Gray Fossil Site, Washington County, in the Southern Appalachian Mountains of eastern Tennessee, USA (36°N, 82°W). Osteoderms of *Heloderma* and other extinct monstersaurians are distinctive within Squamata (see discussions below and in Norell and Gao 1997; Gao and Norell 2000; Nydam 2000; Conrad 2008). Moreover, there is variation in the morphology of the osteoderms among monstersaurian genera, through ontogeny, and in placement on different positions of the body. However, this has never been specified or discussed in detail in the literature (see Bhullar and Smith 2008). Consequently a preliminary discussion concerning this variation is provided below.

A recent study of both mitochondrial and nuclear DNA of the two extant species of *Heloderma* (Douglas et al. 2010) reaffirmed that Helodermatidae are monophyletic, and that it is an ancient and conservative group. A fossil-based constrained date for the origin of Helodermatidae from Douglas et al. (2010) was approximately 106 Ma based on the accepted earliest monstersaurian/helodermatid, *Primaderma*

http://dx.doi.org/10.4202/app.2010.0083

nessovi Nydam, 2000. In addition, the DNA record implies that an initial split of *H. suspectum* Cope, 1869 from a common ancestor with *H. horridum* Wiegmann, 1829 was in the early Eocene (Douglas et al. 2010).

Institutional abbreviations.—ETMNH, East Tennessee State University and General Shale Brick Natural History Museum, Gray, USA; ETVP, East Tennessee State University, Vertebrate Paleontology Laboratory, Department of Geosciences, Johnson City, USA; KUVP, University of Kansas, Vertebrate Paleontology, Lawrence, USA; MNHN, Muséum national d'Histoire naturelle, Paris; TMM, Texas Memorial Museum, Vertebrate Paleontology Laboratory, University of Texas at Austin, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA; UF, University of Florida, Florida Museum of Natural History; USNM, United States National Museum, Smithsonian Institution, Washington, USA.

Geological and geographical settings

The Gray Fossil Site covers an area of about 2.5 ha and contains sediments up to about 40 m thick (Wallace and Wang 2004). Less than five percent of the locality has been systematically excavated, screen-washed, and analyzed. The recovered remains illustrate that the fauna is diverse and abundant, and evidently not fully realized. From elsewhere in North America, the stratigraphic range of *Teleoceras* (rhino) and *Plionarctos* (tremarctine bear) constrain the age of the sediments at the Gray Fossil Site to between 7.0 and 4.5 Ma (latest Miocene–earliest Pliocene), the Hemphillian Land Mammal Age (Wallace and Wang 2004). This age makes the Gray Fossil Site one of the few mid-Neogene vertebrate localities in the eastern United States (Farlow et al. 2001; Tedford et al. 2004).

A wealth of information is becoming available at the Gray Fossil Site; at least 23 species of mammals are currently known from the fauna (with over 80 individuals of the extinct tapir, *Tapirus polkensis*), including *Pristinailurus* (lesser panda), *Arctomeles* (Eurasian badger), in addition to fishes, anurans, salamanders, turtles, *Alligator*, birds, and snakes (Parmalee et al. 2002; Wallace and Wang 2004; Schubert and Wallace 2006; Hulbert et al. 2009). Lizard remains are exceedingly rare, which is perhaps not surprising in that the reconstructed habitat is a forest surrounding a lacustrine basin (DeSantis and Wallace 2008; see below). Even today the temperate deciduous forest, which exists regionally near the Gray Fossil Site, harbors only four species of lizards (Gibbons et al. 2009).

Osteoderms

Terminology.—Osteoderms, especially those fused to cranial elements, are common in monstersaurians, and in some other lizard groups. It is generally assumed that a monstersaurian with cranial osteoderms will also have osteoderms over at least a portion of, if not the entire, body because this is the ancestral condition for Anguimorpha. This is clearly the case in extant *Heloderma*, but osteoderms in fossil taxa are poorly understood. Moreover, osteoderm size and surface texture are difficult to interpret or score as characters (Pregill et al. 1986; Conrad 2008). Consequently, descriptions can be subjective, and terminology varies among authors.

Osteoderms from non-monstersaurians are typically flat (plate-like), predictably thin, and rectangular to trapezoid in shape, as seen in Anguidae (see general descriptions in Hoffstetter 1962; Meszoely and Ford 1976; Strahm and Schwartz 1977; Richter 1994; Mead et al. 1999). Anguine imbricating osteoderms can have intricate sculpturing, some with well-defined keels (Fejérváry-Lángh 1923; Meszoely 1970; Gauthier 1982; Augé 2005). Osteoderms from the Paleogene glyptosaurine anguids of North America and Eurasia (Estes 1983), however, are different showing a pattern of subequal, hexagonal, and sometimes domed plates. Both the cranial and body osteoderms are covered with tubercular mounds, sometimes arranged in concentric patterns (Meszoely et al. 1978; Sullivan 1979; Augé 2005), distinct from the vermiculate network found in monstersaurians, especially *Heloderma*.

Osteoderms from the extinct *Carusia* are similar to those of closely related Xenosauridae (Anguiformes, Carusioidea) in that they cover most skull roofing elements; osteoderms are subdivided into individual elements ornamented with a vermiculate sculpture (Gao and Norell 1998). The row-pattern of scutulation as seen on the extinct xenosaurid *Exostinus* described by Bhullar (2010) appears unique. An individual osteoderm can be portrayed as a "small, peaked lump … [with a] rolling, bumpy sculpture" (Bhullar 2010: 944). The extant, enigmatic anguimorph lizard, *Shinisaurus* has a reduced number of cephalic osteoderms, which are all generally flat, plate-like structures with irregular margins (Bever et al. 2005).

Monstersaurian osteoderms show some consistency; most are circular to polygonal (multilateral) in outline (osteoderms of the tail differ, see below), are not compound structures, and do not have imbricate (overlapping) surfaces, as in many other lizards, especially Cordyloidea and Scinciformes (e.g., see discussion in Richter 1994). Overall appearance of the integument surface on monstersaurians is often described as granular, beadlike, or tuberculate. We use the term "dome" to refer to the individual tubercules. A keel, as in some scincomorphs and anguids, is absent on monstersaurian osteoderms. Cross-sectional shape of helodermatid osteoderms is typically and uniquely domed, or a flattened dome, again giving an overall granular appearance. However, the development of this feature varies in earlier monstersaurians (see below). Surface texture of individual osteoderms, which is important and can vary from different parts of the body, has been termed vermiculate (having wavy or worm-like, sinuous lines). This vermiculate texture on osteoderms can be extreme, creating a pattern of "ridges" and "pits".

Recent monstersaurian osteoderms.—Table 1 provides a list of modern *Heloderma horridum* and *H. suspectum* used in this study. Fig. 1A shows the overall exterior of the cranial and nuchal entegument surface of a typical adult *Heloderma suspectum* (ETVP 7096). Individual osteoderms range from 1.5 to 6.5 mm in diameter on an individual with a snout-vent lengh of 320 mm (ETVP 7083). Typically, osteoderms covering the cranial bones are larger, thicker, and often more polygonal in shape compared to those from the nuchal region or rest of the body, which usually are smaller and have a more circular outline (Fig. 1B; see also *H. horridum* at http://digimorph.org/specimens/Heloderma_horridum/). Some specimens have smaller osteoderms on the parietal region of the cranium, being more similar to those of the nuchal than frontal and lateral sides of the skull. A hatchling *H. suspectum* (ETVP 17869) with a snout-vent length of 125 mm, did not have osteoderms attached to any cranial elements (Fig. 2A). Notice in Fig. 2B (ETVP 17869) the isolated, thin, wafer-like osteoderms have numerous holes, yet already exhibit an incipient domed form, circular-polygonal outline, and vermiculate texture on the apical side of the bone (the term as used here refers to the direction away from the subintegumentary attachment), but lack a basal platform. Fig. 2C shows a close-up of an additional juvenile, *H. horridum* (ETVP 17907), illustrating that the osteoderms form quickly and are already beginning to adhere to cranial bones.

Individual osteoderms characteristically connect to others via tissue; some cranial osteoderms abut others and weakly ossify (Figs. 3A, 4). Osteoderms from the cranium, body, and limbs characteristically (~70% in this study) have a ring-extension (bony flange, cingulum) surrounding, or partly around, the dome (Figs. 3B, 5A, B, D, E). We found no indication in the two extant *Heloderma* species that presence or absence of a ring-extension around the dome is related to the size of the osteoderm or the ontogenetic age of the lizard. No morphological differences were noted between osteoderms of the front and rear limbs. Overall size of osteoderms varies greatly over the body regardless of the snout-vent length of the lizard, and there is no size sorting according to position on the body (i.e., osteoderm size is apparently random). Surface texture of all osteoderms from *Heloderma* is characteristically vermiculate, having the ridge and pit pattern mentioned by Pregill et al. (1986). Incipient vermiculate texture exists in the hatchlings as well adults (compare osteoderms in Figs. 1B, 2B, 3A, B). A keratinous epidermal scale covering on live and unprocessed skeletal specimens can create a smooth appearance to the osteoderm (dark osteoderms in Fig. 1), but texturing of the bone exists below. Osteoderm basal surfaces are typically flat or near-flat (Figs. 4, 5C$_2$, F$_2$).

Superficially, osteoderms of *H. horridum* and *H. suspectum* are similar. Both species have a pattern of ridges and pits, predominantly polygonal cranial osteoderms, and more circular body osteoderms. The pattern of texture on the more robust polygonal cranial osteoderms is repeated on the slightly thiner, circular body osteoderms. However, we did notice that regardless of size or age, the ridge pattern on *H. horridum* routinely develops into acute pinnacles (spicules), providing another level of granular texture to the body and skull (Fig. 3A, B; *H. horridum* ETVP 7081). Ridge texture of *H. suspectum* osteoderms rarely form spicules, giving a more rounded or worn appearance. However, the presence or absence of spicules does not permit a species-level identification of isolated osteoderms. Caudal osteoderms are rectangular in outline and vary from being rather smooth (on the lateral-to-ventral sides of the tail), to having a dome with a slight vermiculate texture (on the dorsal side of the tail; Fig. 3C).

Table 1. Modern specimens used in this study.

Species	Repository number
Heloderma horridum	ETVP 7081
	ETVP 7083
	ETVP 17865
	ETVP 17907
	ETVP 17908
Heloderma suspectum	ETVP 7085
	ETVP 7087
	ETVP 7088
	ETVP 7089
	ETVP 7096
	ETVP 7098
	ETVP 7099
	ETVP 17869

Based on our study of extant *Heloderma* species, we are confident that their osteoderms can be separated into general body regions (i.e., cephalic in part, trunk, tail). Although osteoderm morphology varies by body location, this variation is clearly narrow, meaning that cranial and post-cranial osteoderms are much more similar to each other than to any of the cranial osteoderms in fossil monstersaurian taxa. Further, if extinct monstersaurians were similar to the extant in their osteoderm patterns, we would expect their postcranial and cranial osteoderms to be similar.

Fossil monstersaurian osteoderms.—The earliest known monstersaurian is *Primaderma nessovi* from the Cretaceous (Albian–Cenomanian) of Utah (Nydam 2000). The exterior surface of its maxilla is covered with fused, pitted osteoderms, which are thinner than those of *Heloderma* and *Paraderma* (see below), yet not as plate-like as those in anguids (Nydam 2000: fig. 2). However, variation of *Primaderma* osteoderms is not understood (no body osteoderms are known), although based on the cranial osteoderms, they were presumably not overly domed.

Paraderma bogerti (Estes 1964; Cretaceous, Wyoming), had osteoderms fused to the cranial elements (Fig. 6C). These are relatively large, polygonal in outline, pitted, separated by a wide groove, and "resembled those of *Heloderma*", yet are not quite as granular (Estes 1964: 133). Cranial osteoderms were not domed, but flattened and plate-like (Estes 1964: fig. 64), which is verified by a parietal fragment (Gao and Fox 1996: figs. 34, 35), which shows the pitting but suggests the lack of a vermiculate texture.

http://dx.doi.org/10.4202/app.2010.0083

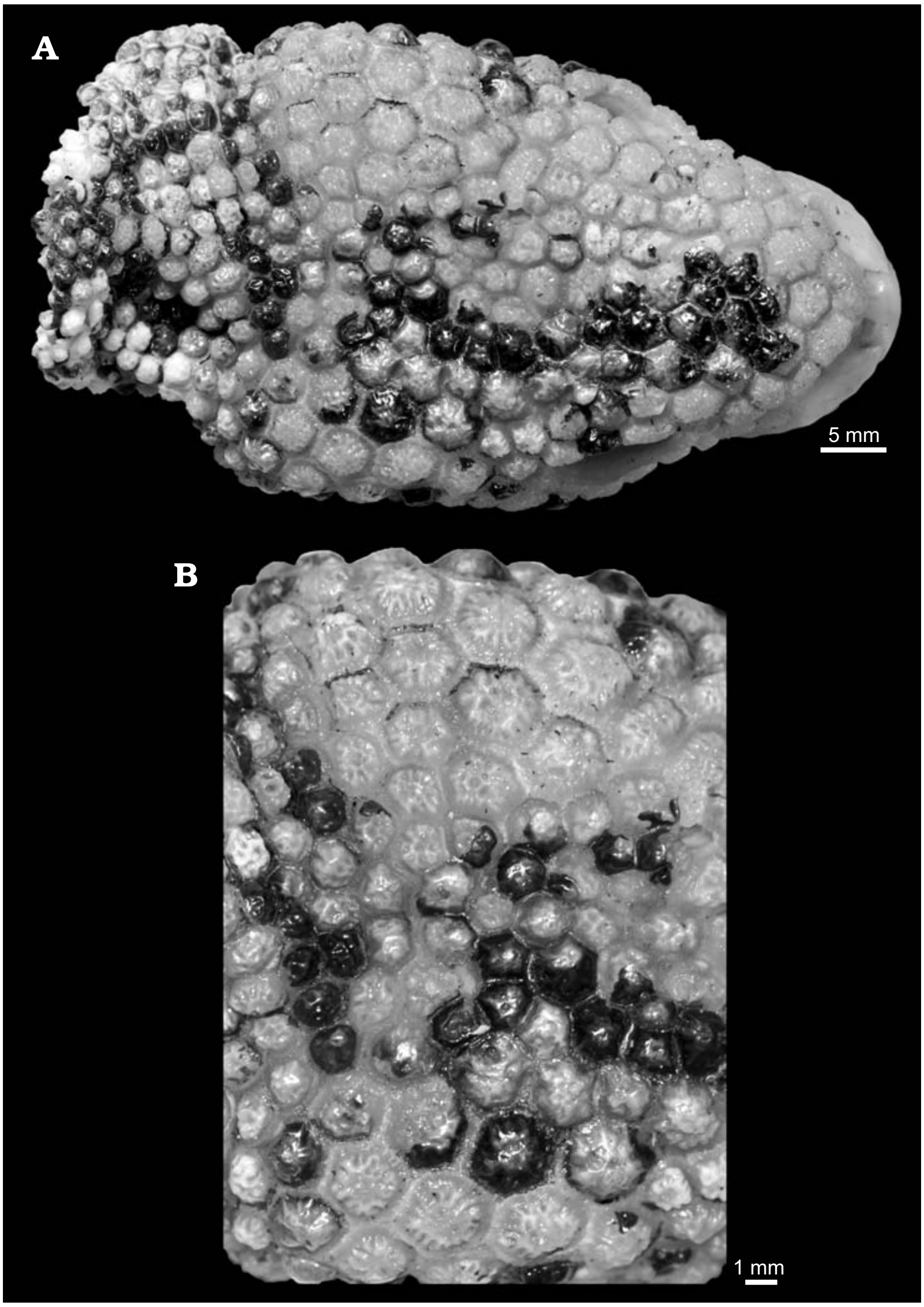

Fig. 1. Extant helodermatid lizard *Heloderma suspectum* Cope, 1869 (ETVP 7096). **A**. An overall appearance of the osteoderm pattern on the cranial and nuchal regions. **B**. A close-up of the osteoderms exemplifying the morphology.

Gobiderma pulchrum (Borsuk-Białynicka 1984: 39) from the Cretaceous of Mongolia had "rounded, perforated osteoderms of *Heloderma* type" (see also Gao and Norell 2000). Cranial osteoderms were fused to the skull and interconnected. Individual elements were somewhat domed yet more plate-like (as in *Primaderma* and *Paraderma*) than those of *Heloderma* (Borsuk-Białynicka 1984: fig. 11; see *Gobiderma pulchrum* at http://digimorph.org/specimens/Gobiderma_pulchrum/).

Osteoderms of *Estesia mongoliensis* (Norell et al. 1992) from the Cretaceous of Mongolia are inadequately known. Originally, it was thought that *Estesia* did not have osteoderms fused to the skull (Norell et al. 1992: table 1, characters 47–48, fig. 13; Gao and Norell 2000). Further examination showed a slight scar-like structure on the supratemporal process that might imply the occurrence of at least some (albeit weak) cranial osteoderms, "but it is indecisive as to whether the osteoderms were platelike or small elements divided by grooves" (Norell and Gao 1997: 24). Based on the apparent lack of well developed osteoderms, *Estesia* need not be considered further in this study (see discussions in Gao and Norell 2000; Conrad 2008).

Eurheloderma gallicum (Hoffstetter 1957; Fig. 6A, B; see also Augé 2005: fig. 181) from the middle/late Eocene of France had granular osteoderms separated by grooves. Not all osteoderms were fused to skeletal elements, suggesting that fusion was likely related to ontogentic growth (Estes 1983). Based on the presence of cranial osteoderms fused to parietal and maxilla, body osteoderms were also probably present, but have not been found. An isolated parietal referred to *Eurheloderma* from the late Paleocene of Wyoming displays dermal rugosities, but the overlying osteoderms did not fuse to the bone, which implies a subadult individual (Pregill et al. 1986). As noted by Pregill et al. (1986: 191), "the parietal ostoderms are largest [relatively] in *Eurheloderma gallicum*, smaller in *Lowesaurus matthewi*, and smaller still in *Heloderma texanum*, and smallest in *H. suspectum* and *H. horridum*." Although the cranial osteoderms have a vermiculate texture, it appears that the large osteoderms of *Eurheloderma* were not domed or flat-domed, and they had a texture similar to those of *Primaderma*, *Paraderma*, and *Gobiderma*. Isolated osteoderms, although rare, are recovered in European deposits, suggesting that more may be learned in the future about the dermal covering of *Eurheloderma* (Augé 1995).

Lowesaurus matthewi, described as *Heloderma* (Gilmore 1928; Pregill et al. 1986) is known from the late Oligocene–early Miocene (Orellan to Arikareean Land Mammal Ages) of Colorado and Nebraska (see also Yatkola 1976). Osteoderms attached to the dorsal surface of the frontal are "shaped like flattened domes", polygonal, separated from one another by moderately deep grooves, and have granular texture; large ones display ridges and pits on the surface (Yatkola 1976: fig. 1; Pregill et al. 1986:183, figs. 4, 6; Fig. 6D, G). Osteoderms of *Lowesaurus* are similar to those of *Heloderma*, with the exception that they are larger, appear less domed, and show no evidence of ring-extensions (Fig. 6D, G).

Heloderma texana (Stevens 1977: 6) from the early Miocene of Texas (Arikareean Land Mammal Age) has hexagonal- to polygonal-shaped, domed osteoderms (some "not as flattened as those in the living species"), many with ring-extensions, and all possess vermiculate textures with ridges and pits (see *H. texana* at http://digimorph.org/specimens/ Heloderma_texana/). These appear near-identical to those of extant *Heloderma*. Although the holotype of *H. texana* (TMM 40635-123) shows some abrasion, we found some evidence of spicules formed in places. Both TMM 40635-123 and 40635-119 have ring-extensions around the osteoderms. The ring-extension around most cranial and body osteoderms appears to occur in all species of *Heloderma*, and so we propose that this is an apomorphy. Stevens (1977) noted that osteoderms of the extinct *H. texana* had deeper pits than in extant species, but we disagree: we find that large *H. horridum* can have osteoderms with deep pits and extreme ridges (e.g., ETVP 7081; Fig. 3A, B). Stevens (1977) determined that the *H. texana* specimen, a mature lizard, was 30–50% the size of adult extant *Heloderma*, thus a distinctly smaller species.

Estes (1963) mentioned that a possible helodermatid vertebra and femur were recovered from the Thomas Farm local fauna of Florida (Hemingfordian Land Mammal Age, early–middle Miocene; Tedford et al. 2004; Richard C. Hulbert personal communication, June 2010; contra Bhullar and Smith 2008). Further work produced additional helodermatid remains, and Bhullar and Smith (2008) concluded that several characters of the dentary were intermediate between *Eurheloderma* and extant *Heloderma*, and therefore did not permit generic identification. A number of isolated osteoderms were recovered with the dentary and found to be round to polygonal in outline; the one pictured has no ring-extension (Bhullar and Smith 2008: fig. 2B). Apical surfaces are highly domed and exhibit a complex network of ridges and pits (i.e., vermiculate). Where many of the ridges connect, they rise to form "small eminences" (= spicules here) (Bhullar and Smith 2008: 291). Our analysis of fourteen additional helodermatid osteoderms from the locality showed that at least six (UF 255289, 255294, 255296, 255297, 255300, 255301) were domed, moderate to heavy with vermiculate sculpturing, most with spicules, and had ring-extensions. With these attributes, we conclude that these osteoderms indicate that *Heloderma* was

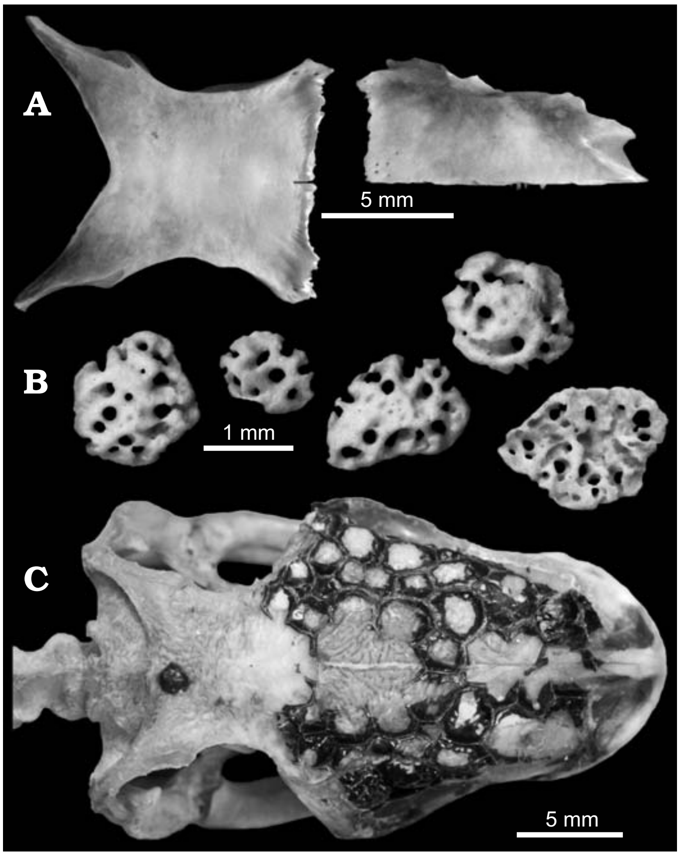

Fig. 2. Extant helodermatid lizard from the USA. **A**. Close-up of *Heloderma suspectum* Cope, 1869 hatchling (ETVP 17869) showing that the frontal and parietal lack fused-on osteoderms (typical of older individuals). **B**. *Heloderma suspectum* Cope, 1869 (hatchling; ETVP 17869). Thin, waffer-like osteoderms have numerous holes yet already show an incipient domed form, polygonal outline, and vermiculate texture on the apical side of the bone (top row) and lacks a basal platform (bottom osteoderm). **C**. Close-up of osteoderms covering portions of the parietal and frontal elements on a juvenile *Heloderma horridum* Wiegmann, 1829 (ETVP 17907).

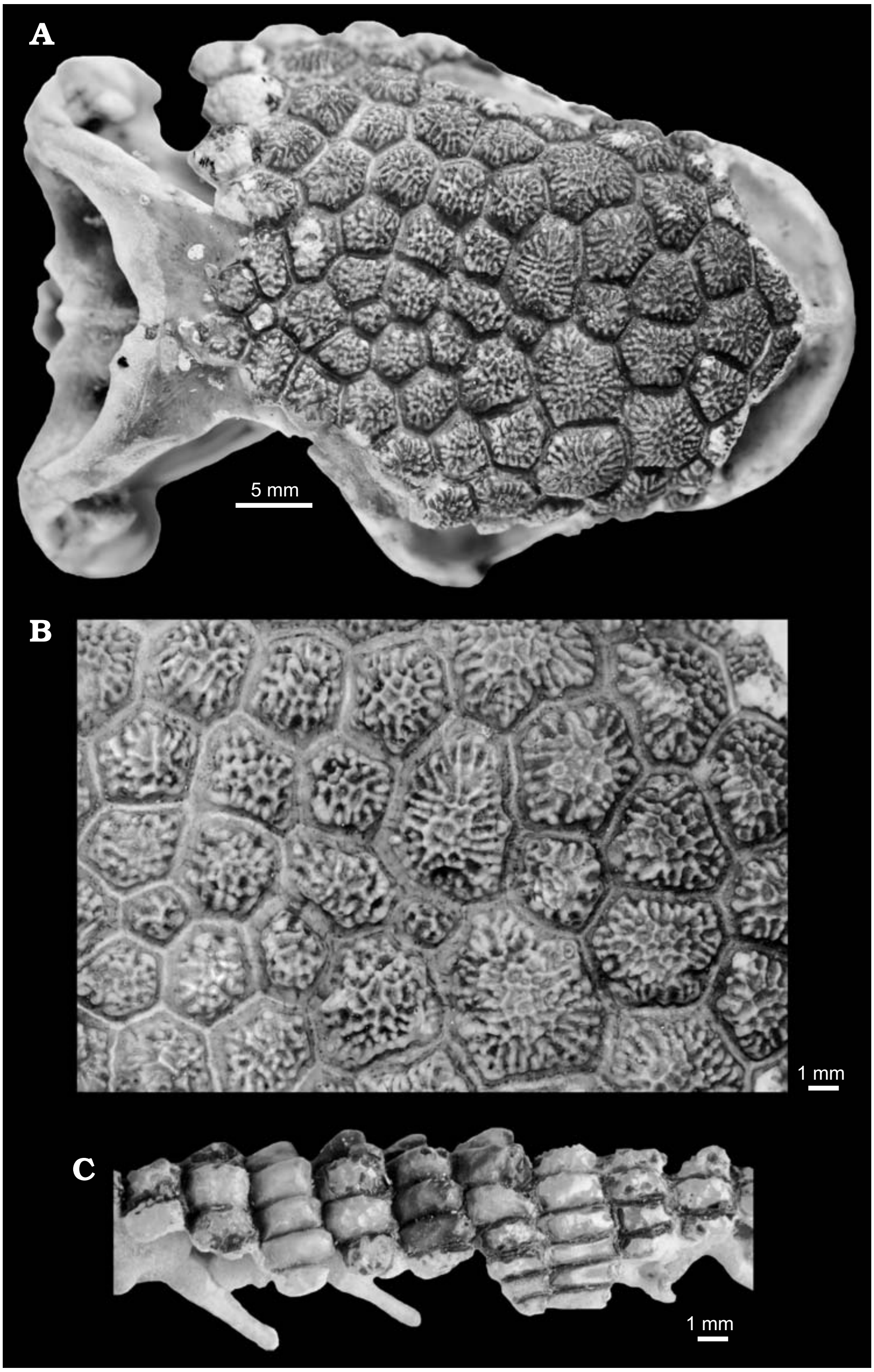

Fig. 3. Extant helodermatid lizard *Heloderma horridum* Wiegmann, 1829 (ETVP 7081). **A**. Cranium showing overall pattern of osteoderms. **B**. Close-up of osteoderms with an acute vermiculate pattern where spicules form on the ridges. **C**. Close-up of the tail vertebrae and overlaying osteoderms.

in Florida at least by the Hemingfordian, early–middle Miocene.

An additional locality in Florida has produced helodermatid remains. Bryant (1991) mentioned the recovery of a single osteoderm from Level 3 at the La Camelia Mine locality of the Willacoochee Creek Fauna (early Barstovian Land Mammal Age; mid-Miocene). Unfortunately the osteoderm was not figured or discussed; our analysis of the specimen was inconclusive.

Gray Fossil Site.—Three isolated osteoderms (ETMNH 8746; Fig. 5A–C_1), distinct in morphology to helodermatid

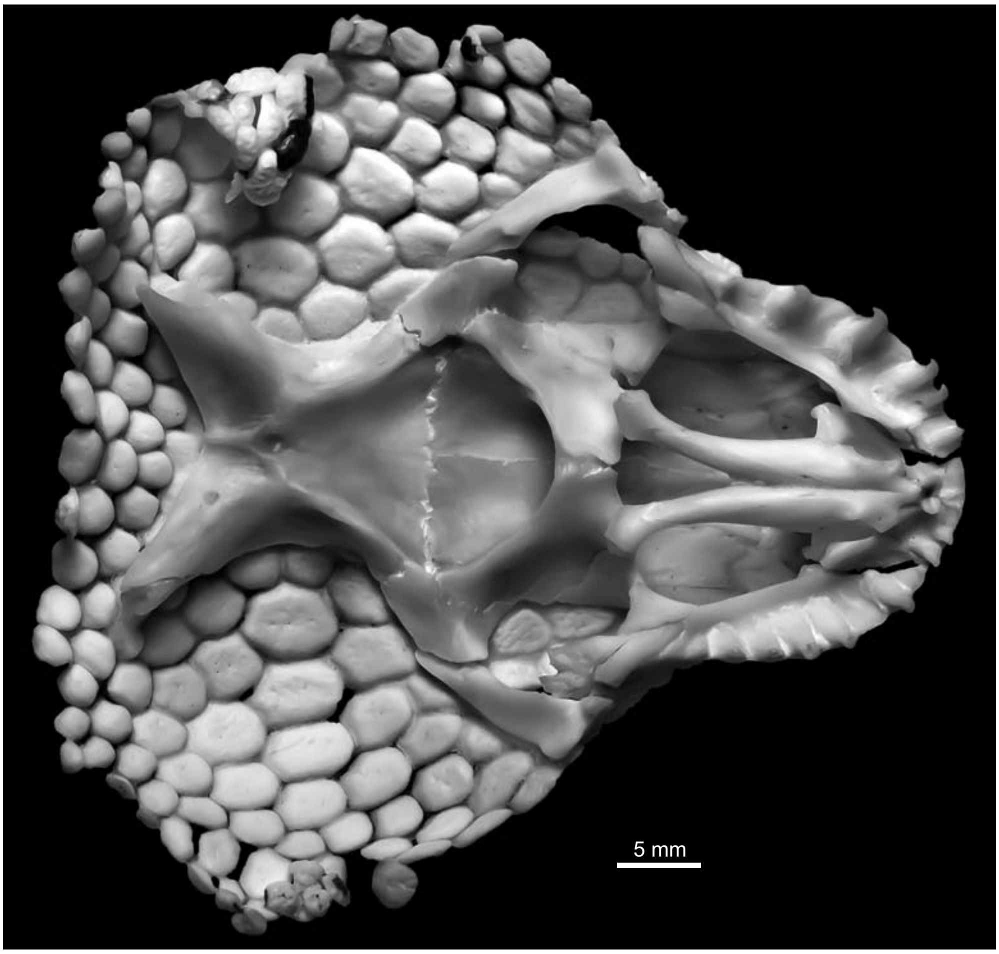

Fig. 4. Ventral view of extant helodermatid lizard *Heloderma suspectum* Cope, 1869, cranium (ETVP 7099) with parietal and frontal in position and adjacent articulated osteoderms showing basal platform, foramina, and tissue attachments between individual elements.

lizards, were recovered (by SLS) from screen-washed sediments from the "Rhino Pit" excavation (TP-2-2004, 365-124 provenance) at the Gray Fossil Site. Additional fossil species from these layers match those found in all other excavation pits from the site. The three osteoderms are whitish in colour, unlike the usual brown to black, indicating that they underwent some weathering in the upper oxidized zone. Some salamander vertebrae and *Tapirus polkensis* elements from the same excavation unit are equally as oxidized and white.

The osteoderms (ETMNH 8746) are small, ranging from 1.5 to 3.0 mm in diameter, and are circular in basal aspect, with a domed apical surface. The basal surface is largely flat, pierced by at least one foramen, and has concentric rings (Fig. 5C_2) that Bhullar and Smith (2008) suggested might relate to growth. The apical, domed surface is vermiculate in texture with a network of pits surrounded by ridges. The lack of a keel or imbricating surfaces indicates that the osteoderms do not come from a scincomorphan or anguid , and the other characters indicate that they come from a monstersaurian.

The three osteoderms (ETMNH 8746) are small and circular and so are not cranial osteoderms (generally more polygonal). In comparison with extant *Heloderma*, they are postcranial, coming anywhere from the neck to the sacrum (Fig. 5D–F_1), but not the tail. Their size and morphology suggests they come from an individual with a snout-vent length of 200 to 350 mm, not an immature individual (< 150 mm snout-vent length). The vermiculate network of ridges and pits on ETMNH 8746 are identical to those found in *Heloderma* and *Lowesaurus*. Two of the osteoderms have a ring-extension around the bone, our proposed apomorphy for *Heloderma* (Fig. 5A–C_1). Two of the three (Fig. 5A, C_1) show the ridge development of spicules as noted especially in extant *H. horridum*, occasionally in *H. suspectum*, and in the Miocene Thomas Farm specimen (discussion above). We identify the Gray Fossil Site osteoderms as *Heloderma*, but cannot go to species level without additional skeletal remains.

Discussion

Shunk et al. (2006) interpreted the depositional environment at Gray Fossil Site as recording storm flow influxes into a paleosinkhole lake. Abundant remains of fishes, neotenic salamanders, aquatic turtles, and numerous *Alligator* specimens confirm a lacustrine environment (Schubert and

http://dx.doi.org/10.4202/app.2010.0083

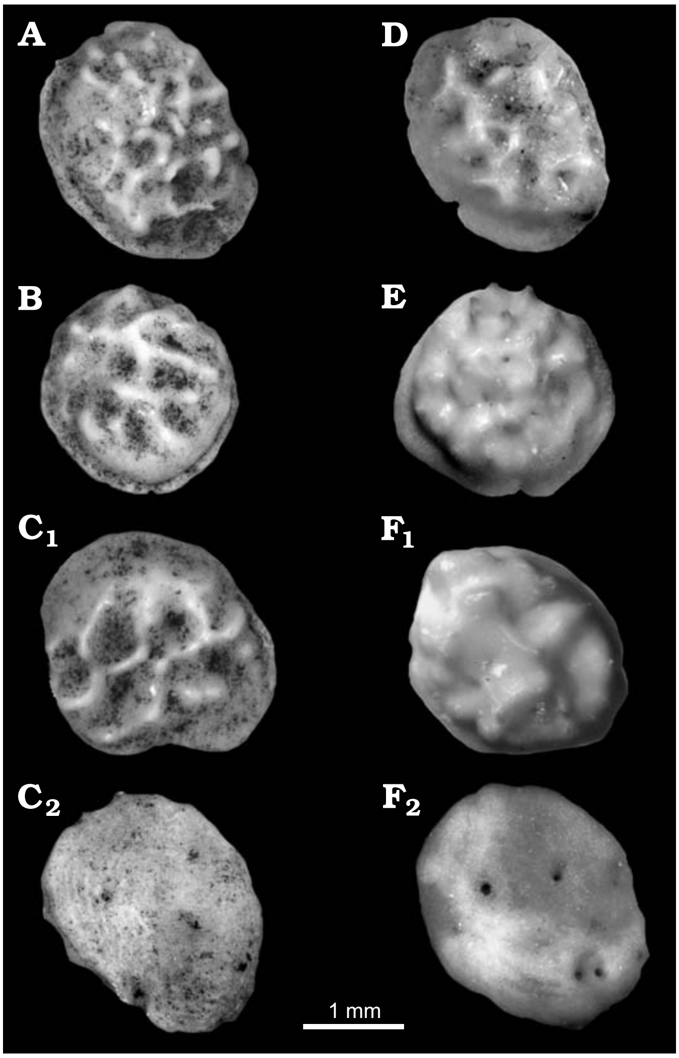

Fig. 5. Osteoderms of the fossil and extant helodermatid lizards from the USA. **A**–**C**. Three osteoderms of *Heloderma* sp. recovered from the "Rhino Pit", Miocene–early Pliocene Gray Fossil Site. **A**. ETMNH 8746a in apical view. **B**. ETMNH 8746b in apical view. **C**. ETMNH 8746c in apical (C_1) and basal (C_2) views. **D**–**F**. Three isolated osteoderms of extant *Heloderma horridum* Wiegmann, 1829 showing varying degrees of a bone ring-extension around the tubercle. **D**. ETVP 7083a in apical view. **E**. ETVP 7083b in apical view. **F**. ETVP 7083c in apical (F_1) and basal (F_2) views.

Wallace 2006; Boardman 2009). Multiple layers of silt and clay, with less common layers of larger clasts, attest to a predominantly low-eneregy aquatic environment, one with at least some through-flow of water. Stable carbon and oxygen isotopes from the bones of browsing mammals indicate a moderately dense forest (C^3 dominated), yet with a grassland (C^4) component nearby, and with minimal seasonal variations in temperature or precipitation (DeSantis and Wallace 2008). Rare Earth Element analysis suggest that at least the mammals shared similar depositional environments, and so were autochthonous (DeSantis and Wallace 2008). Moreover, the rapid infilling of the sinkhole resulted in the preservaton of many articulated or nearly articulated skeletons, implying that it was indeed a biocoenosis.

Macroplant remains from the Gray Fossil Site include at least 35 genera representing more than 25 families of seed plants. These indicate an oak-hickory subtropical forest dominated by *Quercus* (oak) and *Carya* (hickory) with some form of conifer species, an understorey of the *Corylopsis* (buttercup shrub), and the climbing vines *Sinomenium*, *Sargentodoxa*, and *Vitis*. Liu and Jacques (2010) described endocarps belonging to a new species of *Sinomenium* (Menispermaceae; *S. macrocarpum*), today a woody vine confined mostly to lowland tropical or subtropical forests of eastern Asia (Luo et al. 2008). Gong et al. (2010) describe three new species of fossil grapes (*Vitis grayensis, V. lanatoides*, and *V. latisulcata*), two of which closely resemble two Eurasian *Vitis* species implying a strong eastern Asian aspect to the Gray Fossil Site. In addition, pollen recovered from sediments with vertebrates indicates tree/bush species, including *Ulmus* (elm), *Betula* (birch),

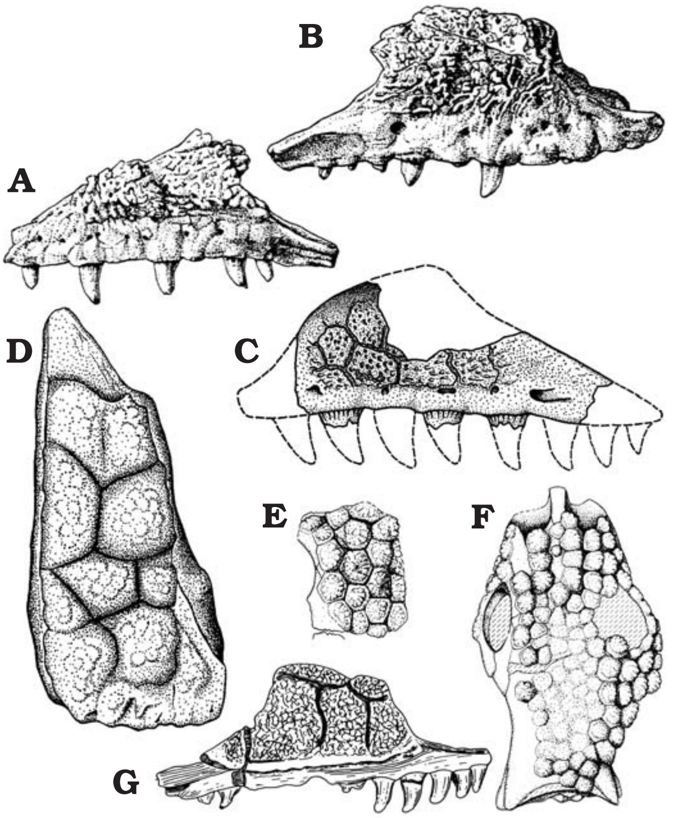

Fig. 6. Various skeletal elements from taxa within Monstersauria illustrating the variation in the osteoderms. **A**, **B**. *Eurheloderma gallicum* Hoffstetter, 1957, Phosphorites du Quercy, France, "san precision de gisement"; maxillae with attached osteoderms. **A**. Left maxilla, unknown specimen number. **B**. Right maxilla, holotype, MNHN; from Hoffstetter 1957; see Augé (2005) for discussion. **C**. *Paraderma bogerti* Estes, 1964, UCMP locality V-5817; maxilla UCMP 542610 with attached osteoderms (from Estes 1964). **D**, **G**. *Lowesaurus matthewi* (Gilmore, 1928) Lewis Creek, Logan County, Colorado, Oreodon Zone, White River formation. **D**. Right frontal, KUVP 49651 showing detail of large osteoderms (from Pregill et al. 1986). **G**. Right maxilla, UNSM 50011 with large fused osteoderms (from Yatkola 1976). **E**, **F**. *Heloderma texana* Stevens, 1977, Castolon Local Fauna, Delaho Formation, Texas. **E**. Cranial bone TMM 40635-119 with fused osteoderms illustrating the ring-extension around the individual osteoderms. **F**. Holotype skull TMM 40635-123.

Fraxinus (ash), *Celtis* (hackberry), *Alnus* (alder), and *Salix* (willow) (Wallace and Wang 2004).

Crocodilians, especially *Alligator*, from the Gray Fossil Site give additional information on the climate (Colbert et al. 1946; Markwick 1998). Today, *Alligator* lives in and survives colder climatic conditions than any other extant crocodilian (Brisbin et al. 1982). The present northern-most extent of *A. mississippiensis* (American alligator) is close to the mean January isotherm of 7.2°C (45°F) and the mean minimum January temperature isotherm of -1°C (34°F). It is the latter metric that limits the present northern range of *A. mississippiensis*. Adult American alligators pass periods of excessive cold temperatures typically in deep water or under vegetation, and extant *A. sinensis* (Chinese alligator) uses burrows to avoid extreme weather. Viable populations of *Alligator* are restricted largely by the greater vulnerability of juveniles and hatchlings than adults to low temperatures (see discussion in Thorbjarnarson and Wang 2010).

Remains of *Alligator* representing many different growth stages are common at the Gray Fossil Site including the area containing *Heloderma*. If they had temperature requirements and restrictions similar to those of the extant species in North America, then we may be able to reconstruct the local temperature regime during the Hemphillian. Using the Nearest Living Relative model of Markwick (1998) indicates a minimum average temperature of the Gray Fossil Site during the Hemphillian of at least ~22°C (71°F) in order to sustain the apparently thriving *Alligator* population. Moreover, the distribution of *Alligator* today does not include the region of the Gray Fossil Site in part because the annual temperature range of 14–29°C (24–84°F) goes too low.

It is not clear whether the reconstructed moderately dense subtropical forest of the Gray Fossil Site during the Hemphillian was wet or dry. The abundant plethodontid salamander vertebrae suggests that the local terrestrial environment was wet enough (precipitation and/or ground litter) for these lungless caudates (Boardman 2009). A number of the Gray Fossil Site plant species have counter-parts in Asia that live in tropical habitats. Stable isotope data suggest minimal variation in temperature or precipitation (DeSantis and Wallace 2008), but there may have been dry and wet seasons (see also discussion in Shunk et al. 2009).

Species of *Heloderma* today are not active at temperatures much below 24°C (75°F; Bogert and Martín del Campo 1956). Their classic habitat is the hot, dry subtropical Sonoran Desert (desert-scrub) of the arid Southwest, but *H. suspectum* also thrives in semidesert grasslands to woodlands. *H. horridum* lives from southern Sonora south along the coastal west side of Mexico to Guatemala, in tropical dry forests, tropical deciduous forests, pine-oak woodlands, and tropical thornscrubs (Bogert and Martín del Campo 1956; Beck 2005). While capable of living in hot arid environments, the genus is most common in tropical deciduous forests where it is known to climb 5–7 m up into trees (Beck 2005). It would appear that such a helodermatid would be equally capable of surviving, if not thriving, in the reconstructed forest of the GFS during the Hemphillian.

The reconstructed warm climate, with either wet or dry, subtropical or tropical habitats in North America during the early to late Miocene extended as far north as the Beringian platform (Wolfe 1994a, b). A tropical forest connection between Asia and North America is also well established (see among others, discussions in Sirkin and Owens 1998; Reinink-Smith and Leopold 2005); however, from the eastern portion of the continent, it is poorly known because of the rarity of localities (Wallace and Wang 2004). The Pipe Creek Sinkhole locality (Indiana; Hemphillian fauna) is interpreted as a ponded sinkhole and the ecological reconstruction is a warm-grassland-woodland transition, but no lizards were recovered (Farlow et al. 2001). The Thomas Farm locality (Florida; Hemingfordian fauna), although earlier than the Gray Fossil Site, is also reconstructed as a sinkhole pond system with a diverse fauna (including some lizards) that inhabited a mixed dry, open country and forested ecotone (Estes 1963).

The Gray Fossil Site provides a unique view of the Mio-Pliocene of eastern North America. Intermixed within the oak-hickory subtropical habitat were faunal components (i) typical of the late Hemphillian of North America, (ii) unique components with distinct Asian affinities, and (iii) now, with the *Heloderma* presented here, taxa presently restricted to arid and tropical environments of Mexico. Clearly the onset of the Plio-Pleistocene cooling events altered the mosaic of floral and faunal species in the communities of the southern Appalachians as well as elsewhere in North America. Tihen (1964: 278–279) presented a then-merging theme, "The present [herpetofaunal] groups inhabitating temperate North America derive from three main sources: (a) relicts of groups that were widespread in the early Tertiary; (b) groups entering from 'the north'—eventually Eurasia—between the mid-Oligocene and mid-Pliocene; (c) groups entering from 'the south'—Central America … this 'southern' contribution is more extensive than is usually realized." Consequently, the *Heloderma* record presented here further corroborates Tihen's model.

Conclusions

Three lizard osteoderms were recovered from the Hemphillian-age (latest Miocene–early Pliocene) sediments at the Gray Fossil Site in northeastern Tennessee. A review of osteoderm morphology of extinct and extant lizards of Monstersauria led to the discovery of a ring-extension that can surround or partly surround the osteosderms of both the cranium and body, character identified here as an apomorphy for *Heloderma*. This genus then once inhabited an oak-hickory subtropical forest surrounding a pond environment that contained abundant remains of fishes, neotenic salamanders, aquatic turtles, and numerous *Alligator*. The forest, with many species of climbing vines, was also inhabited by, among others, species of lesser panda, Eurasian badger,

http://dx.doi.org/10.4202/app.2010.0083

rhino, small bear, sabre-toothed cat, various artiodactyls, multiple terrestrial salamanders, fossorial lizards, snakes, and the beaded lizard *Heloderma*. We show that *Heloderma* was present during the Miocene from at least middle Hemingfordian to the latest Hemphillian Land Mammal Ages in tropical to subtropical environments in southeastern North America.

Acknowledgments

We appreciate the help of Jeff Supplee, Brian Compton, April Nye, Shawn Haugrud, Brett Woodward, and Jeanne Zavada, all members of ETMNH and Gray Fossil Site. We thank Christopher J. Bell (University of Texas at Austin, USA), Randy Nydam (Midwestern University, Glendale, Arizona, USA), and Jozef Klembara (Comenius University in Bratislava, Slovakia) for their continued assistance and discussions about extant and fossil anguimormph lizards. We thank Richard Hulbert (Florida Museum of Natural History, Florida, USA) for the loan of the Thomas Farm helodermatid remains. We appreciate discussions with Yu-Sheng Christopher Liu and Diana Ochoa-Lozano (ETMNH) about the botanical remains recovered from the Gray Fossil Site. Helpful reviews and discussions were received from Marc L. Augé (Muséum national d'Hisitoire naturelle, France), Michael Benton (University of Bristol, UK), Bhart-Anjan S. Bhullar (Harvard University, Massachusetts, USA), and Robert Sullivan (State Museum of Pennsylvania, USA). Partial funding for this project was received from National Science Foundation Award 0958985 to co-authors SCW and BWS.

References

Augé, M. 1995. Un helodermatidé (Reptilia, Lacertilia) dans l'Eocène inféieur de Dormaal, Belgique. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 65: 277–281.

Augé, M. 2005. Evolution des lézards du Paléogène en Europe. *Mémoires du Muséum National d'Histoire Naturelle, Paris* 192: 1–369.

Beck, D.D. 2005. *Biology of Gila Monsters and Beaded Lizards*. 211 pp. University of California Press, Berkeley.

Bever, G.S., Bell, C.J., and Maisano, J.A. 2005. The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). *Palaeontologia Electronica* 8.1.14: 1–36.

Bhullar, B.-A.S. 2010. Cranial osteology of *Exostinus serratus* (Squamata: Anguimorpha), fossil sister taxon to the enigmatic clade *Xenosaurus*. *Zoological Journal of the Linnean Society* 159: 921–953.

Bhullar, B.-A.S. and Smith, K.T. 2008. Helodermatid lizard from the Miocene of Florida, the evolution of the dentary in Helodermatidae, and comments on dentary morphology in Varanoidea. *Journal of Herpetology* 42:286–302.

Boardman, G.S. 2009. *Salamanders of the Mio-Pliocene Gray Fossil Site, Washington County, Tennessee*. 89 pp. Unpublished M.S. thesis, East Tennessee State University, Johnson City.

Bogert, C.M. and Martín del Campo, R. 1956. The gila monster and its allies. The relationships, habits, and behavior of the lizards of the Family Helodermatidae. *Bulletin of the American Museum of Natural History* 109: 1–238.

Borsuk-Białynicka, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. *Palaeontologia Polonica* 46: 5–105.

Brisbin, I.L., Standora, E.A., and Vargo, M.J. 1982. Body temperatures and behavior of American alligators during cold winter weather. *American Midland Naturalist* 107: 209–218.

Bryant, J.D. 1991. New early Barstovian (Middle Miocene) vertebrates from the Upper Torreya Formation, eastern Florida Panhandle. *Journal of Vertebrate Paleontology* 11: 472–489.

Colbert, E.H., Cowles, R.B., and Bogert, C.M. 1946 Temperture tolerances in the American alligator and their bearing on the habits, evolution, and extinction of the dinosaurs. *Bulletin of the American Museum of Natural History* 86: 331–373.

Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History* 310: 1–182.

Cope, E.D. 1869. Diagnosis of *Heloderma suspectum*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 21: 5.

DeSantis, L.R.G. and Wallace, S.C. 2008. Neogene forests from Appalachians of Tennessee, USA: geochemical evidence from fossil mammal teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology* 266: 59–68.

Douglas, M.E., Douglas, M.R., Schuett, G.W., Beck, D.D., and Sullivan, B.K. 2010. Conservation phylogenetics of helodermatid lizards using multiple molecular markers and a supertree approach. *Molecular Phylogenetics and Evolution* 55: 153–167.

Estes, R. 1963. Early Miocene salamanders and lizards from Florida. *Quaterly Journal of the Florida Academy of Sciences* 26: 234–256.

Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation eastern Wyoming. *University of California Publications in Geological Sciences* 49: 1–180.

Estes, R. 1983. Sauria terrestria, Amphisbaenia. *In*: P. Wellnhofer (ed.), *Encyclopedia of Paleoherpetology, Part 10A*, 1–249. Ggustav Fischer Verlag, Stuttgart.

Farlow, J.O., Sunderman, J.A., Havens, J.J., Swinehart, A.L., Holman, J.A., Richards, R.L., Miller, N.G., Martin, R.A., Hunt, R.M., Storrs, G.W., Curry, B.B., Fluegeman, R.H., Dawson, M.R., and Flint, M.E.T. 2001. The Pipe Creek Sinkhole biota, a diverse Late Tertiary continental fossil assemblage from Grand County, Indiana. *American Midland Naturalist* 145: 367–378.

Fejérváry-Lángh, A.M. 1923. Beiträge zu einer Monographie der fossilen Ophisaurier. *Palaeontologia Hungarica, Budapest* 1: 123–220.

Gao, K. and Fox, R.C. 1996. Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of Carnegie Museum of Natural History* 33: 1–107.

Gao, K. and Norell, M.A. 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of anguimorphan lizards. *American Museum Novitates* 3230: 1–51.

Gao, K. and Norell, M.A. 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bulletin of the American Museum of Natural History* 249: 1–118.

Gauthier, J.A. 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contributions to Geology, University of Wyoming* 21 (1): 7–54.

Gibbons, W., Greene, J., and Mills, T. 2009. *Lizards & Crocodilians of the Southeast*. 235 pp. University of Georgia Press, Athens.

Gilmore, C.W. 1928. Fossil lizards of North America. *Memoirs of the National Academy of Sciences* 22: 1–169.

Gong, F., Karsai, I., and Liu, Y.-S. 2010. *Vitis* seeds (Vitaceae) from the late Neogene Gray Fossil Site, northeastern Tennessee, U.S.A. *Review of Palaeobotany and Palynology* 162: 71–83.

Hoffstetter, R. 1957. Un saurien hélodematidé (*Eurheloderma gallicum* nov. gen. et sp.) dans la faune fossile des phosphorites du Quercy. *Bulletin de la Société Géologique de France* 7: 775–786.

Hoffstetter, R. 1962. Observations sur les ostéodermes et la classification des anguidés actuels et fossiles (Reptiles, Sauriens). *Bulletin du Muséum National d'Histoire Naturelle* 34: 149–157.

Hulbert, R.C., Wallace, S.C., Klippel, W.E., and Parmalee, P.W. 2009. Cranial morphology and systematics of an extraordinary sample of the late Neogene dwarf tapir, *Tapirus polkensis* (Olsen). *Journal of Paleontology* 83: 238–262.

Liu, Y.-S. and Jacques, F.M.B. 2010. *Sinomenium macrocarpum* sp. nov.

(Menispermaceae) from the Miocene–Pliocene transition of Gray, northeast Tennessee, USA. *Review of Palaeobotany and Palynology* 159: 112–122.

Luo, S., Chen, T., and Gilbert, M.G. 2008. Menispermaceae. *In*: Z. Wu, P.H. Raven, D. Hong (eds.), *Flora of China, Volume 7: Menispermaceae through Capparaceae*, 1–31. Missouri Botanical Garden Press, St. Louis.

Markwick, P.J. 1998. Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 137: 205–271.

McDowell, S.B. and Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorphan lizards. *Bulletin of the American Museum of Natural History* 105: 1–142.

Mead, J.I., Arroyo-Cabrales, J., and Johnson, E. 1999. Pleistocene lizards (Reptilia: Squamata) from San Josecito Cave, Nuevo León, México. *Copeia* 1999: 163–173.

Meszoely, C.A.M. 1970. North American fossil anguid lizards. *Bulletin of the Museum of Comparative Zoology* 139 (2): 87–149.

Meszoely, C.A.M. and Ford, R.L.E. 1976. Eocene glasslizard *Ophisaurus* (Anguidae) from the British islands. *Copeia* 1976: 407–408.

Meszoely, C.A.M. , Estes, R., and Haubold, H. 1978. Eocene anguid lizards from Europe and a revision of the genus *Xestops*. *Herpetologica* 34 (2): 156–166.

Norell, M.A. and Gao, K.-Q. 1997. Braincase and the phylogenetic relationships of *Estesia mongoliensis* from the Late Cretaceous of the Gobi Desert and the recognition of a new clade of lizards. *American Museum Novitates* 3211: 1–25.

Norell, M.A., McKenna, M.C., and Novacek, M.J. 1992. *Estesia mongoliensis*, a new fossil varanoid from the Late Cretaceous Barun Goyot Formation of Mongolia. *American Museum Novitates* 3045: 1–24.

Nydam, R.L. 2000. A new taxon of helodermatid-like lizard from the Albian–Cenomanian of Utah. *Journal of Vertebrate Paleontology* 20: 285–294.

Parmalee, P.W., Klippel, W.E., Meylan, P.A., and Holman, J.A. 2002. A late Miocene–early Pliocene population of *Trachemys* (Testudines: Emydidae) from east Tennessee. *Annals of Carnegie Museum* 71: 233–239.

Pregill, G.K., Gauthier, J.A., and Greene, H.W. 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Transactions of the San Diego Society of Natural History* 21: 167–202.

Reinink-Smith, L.M. and Leopold, E.B. 2005. Warm climate in the Late Miocene of the South Coast of Alaska and the occurrence of Podocarpaceae pollen. *Palynology* 29: 205–262.

Richter, A. 1994. Lacertilia aus der Unteren Kreide von Uña und Galve (Spanien) und Anoual (Marokko). *Berliner Geowissenschaftliche Abhandlungen E* 14:1–147.

Schubert, B. and Wallace, S.C. 2006. Amphibians and reptiles of the Mio-Pliocene Gray Fossil Site and their paleoecological implications. *Journal of Vertebrate Paleontology* 26 (3 supplement): 122A.

Sirkin, L. and Owens, J.P. 1998. Palynology of latest Neogene (Middle Miocene to Late Pliocene) strata in the Delmarva Peninsula of Maryland and Virgina. *Northeastern Geology and Environmental Geology* 20: 117–132.

Shunk, A.J., Driese, S.G., and Clark, G.M. 2006. Latest Miocene to earliest Pliocene sedimentation and climate record deerived from paleosinkhole fill deposits, Gray Fossil Site, northeastern Tennessee, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology* 231: 265–278.

Shunk, A.J., Driese, S.G., and Dunbar, J.A. 2009. Late Tertiary paleoclimatic interpretation from lacustrine rhythmites in the Gray Fossil Site, northeastern Tennessee, USA. *Journal of Paleolimnology* 42: 11–24.

Strahm, M.H. and Schwartz, A. 1977. Osteoderms in the anguid lizard subfamily Diploglossinae and their taxonomic importance. *Biotropica* 9: 58–72.

Stevens, M.S. 1977. Further study of Castolon local fauna (Early Miocene), Big Bend National Park, Texas. *Pearce-Sellards Series, Texas Memorial Museum* 28: 1–69.

Sullivan, R.M. 1979. Revision of the Paleogene genus *Glyptosaurus* (Reptilia, Anguidae). *Bulletin of the American Museum of Natural History* 163 (1): 1–72.

Tedford, R.H., Albright, L.B., Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt, R.M., Storer, J.E., Swisher, C.C., Voorhies, M.R., Webb, S.D., and Whistler, D.P. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (Late Oligocene through early Pliocene epochs). *In*: M.O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America. Biostratigraphy and Geochronology*, 169–231. Columbia University Press, New York.

Thorbjarnarson, J. and Wang, X. 2010. *The Chinese Alligator. Ecology, Behavior, Conservation, and Culture*. 265 pp. Johns Hopkins University Press, Baltimore.

Tihen, J.A. 1964. Tertiary changes in the herpetofaunas of temperate North America. *Senckenbergiana biologica* 45: 265–279.

Wallace, S.C. and Wang, X. 2004. Two new carnivores from an unusual late Tertiary forest biota in eastern North America. *Nature* 431: 556–559.

Wiegmann, A.F.A. 1829. Ueber das Acaltetepan oder Temaculcahua des Hernandez, eine neue Gattung der Saurier, *Heloderma*. *Isis von Oken* 22: 624–629.

Wolfe, J.A. 1994a. Tertiary climatic changes at middle latitudes of western North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108: 195–205.

Wolfe, J.A. 1994b. An analysis of Neogene climates in Beringia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108: 207–216.

Yatkola, D.A. 1976. Fossil *Heloderma* (Reptilia, Helodermatidae). *Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas* 51: 1–14.

http://dx.doi.org/10.4202/app.2010.0083