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

Authors: Jim I. Mead, Blaine W. Schubert, Steven C. Wallace, and Sandra L. Swift
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
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*). 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, permitting 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, BLAINE W. SCHUBERT, STEVEN C. WALLACE, and SANDRA L. SWIFT

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

**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 *Pristinaulurus* (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; Meszöly 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-Láng 1923; Meszöly 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 (Meszöly 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 (Anguimorphs, 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 length 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 hatching *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 api- cal 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 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, F2).

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 thinner, 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).

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 postcrania and cranial osteoderms to be similar.

Fossil monstersaurian osteoderms.—The earliest known monstersaurian is *Primaderma nesovii* 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.

Table 1. Modern specimens used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Repository number</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Heloderma horridum</em></td>
<td>ETVP 7081</td>
</tr>
<tr>
<td></td>
<td>ETVP 7083</td>
</tr>
<tr>
<td></td>
<td>ETVP 17865</td>
</tr>
<tr>
<td></td>
<td>ETVP 17907</td>
</tr>
<tr>
<td></td>
<td>ETVP 17908</td>
</tr>
<tr>
<td><em>Heloderma suspectum</em></td>
<td>ETVP 7085</td>
</tr>
<tr>
<td></td>
<td>ETVP 7087</td>
</tr>
<tr>
<td></td>
<td>ETVP 7088</td>
</tr>
<tr>
<td></td>
<td>ETVP 7089</td>
</tr>
<tr>
<td></td>
<td>ETVP 7096</td>
</tr>
<tr>
<td></td>
<td>ETVP 7098</td>
</tr>
<tr>
<td></td>
<td>ETVP 7099</td>
</tr>
<tr>
<td></td>
<td>ETVP 17869</td>
</tr>
</tbody>
</table>

http://dx.doi.org/10.4202/app.2010.0083
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 ontogenetic 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 osteoderms 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 vertebral elements on a juvenile Heloderma horridum Wiegmann, 1829 (ETVP 17907). 40635-123 and 40635-119 have ring-extensions around the bone, which implies a subadult individual (Pregill et al. 1986). As noted by Pregill et al. (1986: 191), “the parietal osteoderms 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, 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
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), distinct in morphology to helodermatid

---

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.
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) 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), but not the tail. Their size and morphology suggest 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 Lovesaurus. Two of the osteoderms have a ring-extension around the bone, our proposed apomorphy for Heloderma (Fig. 5A–C). Two of the three (Fig. 5A, C) 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
Wallace 2006; Boardman 2009). Multiple layers of silt and clay, with less common layers of larger clasts, attest to a predominantly low-energy 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 (C3 dominated), yet with a grassland (C4) 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 preservation 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),
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; Reinkink-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 Miocene of eastern North America. Intermixed within the oakhickory 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 inhabiting 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 Monstrosauria led to the discovery of a ring-extension that can surround or partly surround the osteoderms 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,
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 anguimorph 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’Histoire 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**


Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Forma−


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


