CONTRIBUTIONS IN SCIENCE

COLOR PATTERN ON THE SELMACRYPTODIRAN TURTLE *NEURANKYLUS* FROM THE EARLY PALEOCENE (PUERCAN) OF THE SAN JUAN BASIN, NEW MEXICO

Robert M. Sullivan, Spencer G. Lucas,
Adrian P. Hunt, and Thomas H. Fritts
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COLOR PATTERN ON THE SELMACRYPTODIRAN TURTLE
NEURANKYLUS FROM THE EARLY PALEOCENE (PUERCAN)
OF THE SAN JUAN BASIN, NEW MEXICO

Robert M. Sullivan,¹ Spencer G. Lucas,²
Adrian P. Hunt,³ and Thomas H. Fritts⁴

ABSTRACT. A specimen of an early Paleocene selmacryptodiran turtle *Neurankylus*, cf. *N. eximius*, from the Nacimiento Formation, San Juan Basin, New Mexico, is the first specimen of a fossil turtle known in which the altered keratinous epidermal scale covering and the original color pattern of the carapace is preserved. The color pattern of this 63-million-year-old freshwater turtle consists of black spots surrounded by a reddish-brown matrix. Electron microbeam analysis of the altered keratinous layer that retains the color indicates that its composition is principally iron. Comparison of the color pattern with that of extant turtles is consistent with sedimentological and osteological evidence that suggests *Neurankylus* was a large, benthic turtle that favored standing bodies of water during the Late Cretaceous and Paleocene.

INTRODUCTION

Fossil turtles are a common component of the Late Cretaceous and early Cenozoic vertebrate faunas of the Western Interior. Their remains have been collected for more than one hundred years from an area that stretches from the northern Canadian plains to the lower reaches of northern New Mexico. However, despite the thousands of specimens that have been collected and catalogued by universities and museums, most of these fossil chelonians are fragmentary and defy precise identification below the “family” or genus level.

Paleocene turtles from the Nacimiento Formation, San Juan Basin, New Mexico (Fig. 1) are no exception. Few complete specimens are known, and most consist of isolated carapace and/or plastron fragments. Paleocene fossil turtles from the San Juan Basin were first reported by Cope (1888), who named *Hoplochelys crassa* from the Nacimiento Formation based on fragments of the carapace and plastron. Hay (1908) and Gilmore (1919) described many taxa from the Nacimiento Formation that were recently discussed briefly by Sullivan and Lucas (1986). Because many of these species were based on incomplete material, many of the early Paleocene turtle taxa from the San Juan Basin are certainly *nomina dubia* (see Sullivan and Lucas, 1986, for discussion and review of taxa).

Here we describe a unique, nearly complete Paleocene turtle shell identified as *Neurankylus*, cf. *N. eximius*, paying special attention to its keratinous epidermal scales and color pattern. To our knowledge, no fossil turtle that preserves the original, keratinous epidermal carapace-covering has been reported previously. The only previous report of a trace of color on a fossil turtle was made by Holman and Sullivan (1981), who described peripheral pigmentation by dark ocellar markings on a late Miocene (Barstovian) specimen of *Chrysemys picta* from Nebraska. However, this turtle lacked the epidermal scale-covering that is preserved on the carapace of the specimen described herein.

METHODS AND MATERIALS

We follow the classification of Gaffney (1972) and Gaffney et al. (1987), in part, in our systematic presentation for *Neurankylus*. We also follow Gauthier et al. (1988) in not recognizing formal higher taxonomic categories.

In our electron microbeam analysis of the preserved epidermal covering (see below), a thin section approximately 30 μm thick was cut from a fragment of the carapace of LACM 127773 that preserved the color pattern (Fig. 2b). The section was ground using a sequence of grits, the smallest being 0.25 μm, and double polished. It was coated with carbon using a Denton Vacuum DV-590 Evaporator and

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SYSTEMATICS
Testudines Linnaeus, 1758
Casichelydia Gaffney, 1975
Cryptodira (Cope, 1868)
Selmacryptodira Gaffney, Hutchison, Jenkins, and Meeker, 1987
Genus Neurankylus Lambe, 1902

TYPE SPECIES. Neurankylus eximius Lambe, 1902:42.

DISTRIBUTION. (Revised after Gaffney, 1972.) Campa-
lian of Alberta and New Mexico; Maastrichtian of Mon-
tana; ?Maastrichtian of Wyoming; earliest Paleocene (Puer-
can) of New Mexico and Montana; late-early Paleocene (Torrejonian) of New Mexico.


DISCUSSION. Only one species of Neurankylus, N. ex-
imius, is currently recognized (Gaffney, 1972). Some speci-
mens of N. eximius possess keeled neurals. However, this
feature appears to be either lost in Paleocene forms and/or
variable. It thus seems best not to consider this a diagnostic
feature of the genus. The Paleocene specimens from the Puer-
can interval (LACM 127773) and the Torrejonian interval
(UNM NP-010) in the San Juan Basin do not have keeled
neurals. Based on this observation, the characteristics offered
by Gaffney (1972), and taxonomic conclusions recently drawn
by Hutchison and Archibald (1986), we consider LACM
127773 to be referable to Neurankylus (see discussion below).

Neurankylus, cf. N. eximius

REFERRED SPECIMEN. LACM 127773, nearly com-
plete articulated carapace and plastron with epidermal car-
apace covering (Figs. 2, 3).

LOCALITY. De-na-zin Wash, LACM 5533, center of
SW4/4, NW4/4, SW4/4, Sec. 10, T24N, R11W, San Juan County,
New Mexico (Fig. 1).

HORIZON AND AGE. "Puero Interval," approximately
10 m above the base of the Nacimiento Formation in green-
ish-white, sandy mudstone, Nacimiento Formation (earliest
Paleocene).

DESCRIPTION. The carapace (Figs. 2a, b) is oval in shape
and measures 590 mm in length and 470 mm in width.
Although articulated, the carapace is dorsoventrally com-
pressed, severely fractured, and bound together along frac-
tures by silty mudstone. The carapace is, for the most part,
smooth, and the posterior edge lacks emargination but is
scalloped. No sulci or sutures can be identified on the car-
apace largely because most of the carapace is covered by
epidermal scale-layer (Fig. 2b).

The epidermal scales are preserved on approximately 85% of
the carapace, and this epidermal layer is the most signif-
icant feature of this specimen. The epidermal keratinous cov-
ering has been partially removed by weathering along the left
margin of the carapace. The epidermal scales are not pre-
served on the plastron. The original color pattern of the

ABBREVIATIONS
LACM Natural History Museum of Los Angeles County,
Los Angeles, California
UCMP University of California Museum of Paleontol-
ogy, Berkeley, California
UNM University of New Mexico, Department of Geo-
logy, Albuquerque, New Mexico
UNM SB University of New Mexico, Department of Bi-
ology, Museum of Southwestern Biology, Al-
buquerque, New Mexico

Sullivan, Lucas, Hunt and Fritts: Neurankylus color pattern
Figure 2. Neurankylus, cf. N. eximius (LACM 127773). Nearly complete shell: a and b, dorsal view of carapace; c and d, ventral view of plastron and carapace.
Figure 3. *Neuranylus*, cf. *N. eximius* (LACM 127773). Close-up photograph showing part of the carapace that has preserved the color pattern (see Fig. 2b for location of this photograph on the carapace).
epidermal keratinous layer is preserved as a result of preservation of the epidermal layer itself (see later discussion). The carapace coloring (Fig. 3) consists of moderate to dark, reddish-brown (10 R 3/4–10 R 4/6) matrix with black (N1) spots (colors are those of Goddard et al., 1979). The spots range in diameter from 2 to 5 mm. Spacing between the spots varies from 1 to 6 mm. The intensity and clarity of the color pattern varies topographically on the carapace and is best preserved along the midline and posterior parts (Fig. 2b).

The epipleural length is 470 mm. The anterior lobe length is 110 mm and that of the posterior lobe is 140 mm. The shape of the plastron (Figs. 2c, d) conforms to that of Neurankylus eximius (cf. Gaffney, 1972:fig. 38a). The outlines of nearly all the epidermal scales (sulci) and sutures of the plastron are not discernible owing to fusion; only a few sulci can be discerned.

**DISCUSSION.** LACM 127773 is referred to the genus Neurankylus based on characters 1, 2, 4, 9, 11 cited by Gaffney (1972:291). In addition, other features noted by Archibald (pers. comm., 1987), such as the fusion of the carapace and plastron, obliterating the sulci and sutures, support reference to the taxon Neurankylus.

Lucas (1982) cited the occurrence of Neurankylus (UNM NP-010) from the late-early Paleocene (Torrejonian) of New Mexico. This specimen, although incomplete, has enough characters to confidently refer it to Neurankylus. Furthermore, the fact that some sutures and sulci are visible on both the carapace and plastron, and that the measurements are somewhat inconsistent with those of other specimens of Neurankylus (see Table 1), suggest that it may represent a sub-adult individual. Assuming that the measurements are of adult individuals, except for UNM NP-010, it appears that there is an increase in size through time in Neurankylus.

Only recently has the genus Neurankylus been recognized in strata younger than Late Cretaceous. Hutchison and Archibald (1986) reported Neurankylus from the earliest Paleocene (Puercan) age Tullock Formation of Montana, and Lucas (1982) noted the occurrence of Neurankylus in the late-early Paleocene (Torrejonian) interval of the Nacimiento Formation, San Juan Basin. Recovery of LACM 127773 from the Puercan interval of the Nacimiento Formation thus adds to the post-Cretaceous distribution of Neurankylus.

### ELECTRON MICROBEAM ANALYSIS OF THE PRESERVED EPIDERMAL COVERING

SEM imaging indicates that the carapace of LACM 127773 is zoned parallel to the surface of the carapace (Fig. 4a). The layer containing the color (Layer 1) is slightly variable in thickness, averaging about 475 μm. This layer has a nearly flat exterior, but the interior surface is variable. Portions of this surface are smooth, but in most places Layer 1 intrudes into the underlying bone through complex and irregular veins averaging 10 μm in diameter with the largest being 250 μm wide. In one part of the specimen, a distinct area of mottled color lies exterior to the more normal Layer 1. This area is approximately 2500 μm long and 500 μm thick and was treated separately for EDS analysis.

#### Table 1. Shell measurements of Neurankylus. A, ratios of two Paleocene specimens (LACM 127773 and UNM NP-010) compared to ranges derived from Late Cretaceous specimens cited by Archibald (pers. comm., 1987). B, measurements of two Late Cretaceous specimens (UCMP 117103 and LACM 42730) from the Hell Creek Formation (Lancian), Montana, and two Paleocene specimens (LACM 127773 and UNM NP-010) from the Nacimiento Formation (Puercan and Torrejonian, respectively), New Mexico.

<table>
<thead>
<tr>
<th></th>
<th>Neurankylus</th>
<th>LACM 127773</th>
<th>UNM NP-010</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anterior lobe length/posterior lobe length</td>
<td>0.79–0.94</td>
<td>0.79</td>
<td>0.82</td>
</tr>
<tr>
<td>Plastron length/carpapace length</td>
<td>0.87–0.89</td>
<td>0.79</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>UCMP 11703</td>
<td>LACM 42730</td>
<td>UNM NP-010</td>
</tr>
<tr>
<td>Anterior lobe length</td>
<td>95 mm</td>
<td>105 mm</td>
<td>115 mm</td>
</tr>
<tr>
<td>Posterior lobe length</td>
<td>120 mm</td>
<td>130 mm</td>
<td>140 mm</td>
</tr>
<tr>
<td>Plastron length</td>
<td>380 mm</td>
<td>420 mm</td>
<td>420 mm</td>
</tr>
<tr>
<td>Carapace length</td>
<td>?</td>
<td>?</td>
<td>520 mm</td>
</tr>
</tbody>
</table>

The second layer (Fig. 4a, Layer 2) represents the exterior of the bony carapace and consists of a homogeneous zone about 1250 μm thick. This layer is punctuated by veinlets of material similar to that in Layer 1, one of which follows a very linear pathway, and small irregularly spaced lacunae with similar infillings.

The innermost layer (Fig. 4a, Layer 3), of which about 1000 μm are preserved, consists of bone punctuated by many lacunae that are filled by material similar to that found in Layer 1. The lacunae are subvoid in shape, with long dimensions averaging 125 μm and are separated by areas of solid bone that are 100–200 μm wide.

A series of eight EDS point analyses were run on a transect perpendicular to the carapace margins. This sampling included analyses of internal and external areas of Layer 1, bone and a lacuna infilling in Layer 3, and the light and dark portions of the mottled area (Table 2). The EDS analyses indicate that four different compounds are present in the sample constituting Layer 1, lacunae infillings in Layers 2 and 3, and Layers 2 and 3 and the light fraction in the mottled area (Table 2).

Layer 1 is composed of a compound rich in iron, manganese, silicon, calcium, and aluminum (Table 2). The composition of this layer is variable, but is distinct from other parts of the sample. The dark material that infills lacunae in Layers 2 and 3 and constitutes the dark portion of the mottled area is similar to that in Layer 1. However, Layer 1 contains less than 30% of the iron in the other dark material, and with one exception less than 26% of the manganese. Both materials are similar in lacking phosphorus and containing relatively high amounts of iron, manganese, and silicon. One analysis

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of a lacuna infilling in Layer 2 has anomalous amounts of sulfur.

Analyses of bone from Layers 2 and 3 show a constant composition with calcium:phosphorus ratios averaging 1:0.48 (n = 3). Iron, manganese, and sulfur are present in variable trace amounts and are presumably replacing calcium and carbon, respectively, in the collophane formula (Rogers, 1924). The other distinct compound constitutes the light portion of the mottled area. This material contains no calcium, large amounts of silicon, and trace amounts of iron with a silicon:iron ratio of 96:64:1.

In all cases, the boundaries between areas of different composition are sharp. Elemental dot-maps for calcium and iron (Figs. 4b, c) demonstrate that the majority of the specimen is composed of calcium-rich bone and iron-rich material in Layer 1 and infillings in Layers 2 and 3. The elemental analyses of the bone are consistent with previous work that indicates that fossil bone is usually composed of collophane, a complex compound of calcium, phosphorus, carbon, hydrogen, and oxygen (Rogers, 1924; Jaffee and Sherwood, 1951). The siliceous material in the mottled area is a form of silica, which is common as a void-filling in fossil bone (Rogers, 1924; Parker and Toots, 1970).

The material that constitutes Layer 1 and infills most of the voids is very rich in iron. This element is common in fossil bone, as a diagenetic product in open pores and fractures (Paine, 1937; Houston et al., 1966; Parker, 1968; Parker and Toots, 1970). Parker and Toots (1970: fig. 2) illustrated an elemental dot-map of a piece of Miocene turtle bone showing the restriction to open pores. Iron is particularly common in bones of Paleocene and Eocene age (Houston, 1962; Toots, 1963; Houston et al., 1966; Clark et al., 1967). The random distribution of iron in fossil bone was reviewed at length by Houston et al. (1966), who concluded that high iron content indicates a warm humid climate.

EDS analyses suggest that LACM 127773 underwent four phases of diagenesis: (a) alteration of bone material to collophane; (b) alteration or replacement of the epidermal layer (Layer 1); (c) infilling of large lacunae by an iron-rich compound; (d) infilling of small lacunae by silica. Given the similarity between the composition of Layer 1 and the material infilling the large voids, the origin of these two materials may be related.

The specimen of extant Pseudemys concinna (UNM SB 42696) is approximately 1100 μm thick and has a zonation parallel to the carapace margin analogous to that seen in LACM 127773 (Fig. 5). The outer layer (Layer 1) is the epidermal layer that preserved the color pattern. Layer 1 varies in thickness from 20 to 50 μm and parallels the slightly

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Table 2. Proportional peak heights of x-ray intensities from EDS analysis of polished section of carapace of Neurankylus, cf. N. eximius (LACM 127773). Proportions are relative to calcium and reflect relative abundance of the element listed.

<table>
<thead>
<tr>
<th>Site</th>
<th>Ca Ka</th>
<th>P Ka</th>
<th>Fe Ka</th>
<th>Mn Ka</th>
<th>Si Ka</th>
<th>S Ka</th>
<th>Al Ka</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outer part of Layer 1</td>
<td>1</td>
<td>-</td>
<td>1.95</td>
<td>0.90</td>
<td>0.49</td>
<td>-</td>
<td>0.074</td>
</tr>
<tr>
<td>Inner part of Layer 1</td>
<td>1</td>
<td>-</td>
<td>5.58</td>
<td>1.72</td>
<td>2.48</td>
<td>-</td>
<td>0.71</td>
</tr>
<tr>
<td>Infilling of lacuna in Layer 2</td>
<td>1</td>
<td>-</td>
<td>21.28</td>
<td>0.66</td>
<td>2.39</td>
<td>21.51</td>
<td>-</td>
</tr>
<tr>
<td>Infilling of lacuna in Layer 3</td>
<td>1</td>
<td>-</td>
<td>19.04</td>
<td>7.14</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mottled area*</td>
<td>1</td>
<td>-</td>
<td>24.14</td>
<td>6.80</td>
<td>2.38</td>
<td>-</td>
<td>0.69</td>
</tr>
</tbody>
</table>

Layer 2 bone 1: 0.49 Layer 2 bone 1: 0.46 0.083 0.026 0.012 Layer 3 bone 1: 0.48 - 0.015

* Dark-light part of mottled area has Si:Fe of 96.64:1.
Table 3. Proportional peak heights of x-ray intensities from EDS analysis of polished section of Pseudemys concinna (UNM SB 42696). Proportions are relative to calcium and reflect relative abundances of the element listed.

<table>
<thead>
<tr>
<th>Site</th>
<th>Ca (Kα)</th>
<th>P (Kα)</th>
<th>S (Kα)</th>
<th>Si (Kα)</th>
<th>Mg (Kα)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Layer 1</td>
<td>1</td>
<td>0.49</td>
<td>0.082</td>
<td>0.070</td>
<td>-</td>
</tr>
<tr>
<td>Layer 1</td>
<td>1</td>
<td>0.45</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Layer 1</td>
<td>1</td>
<td>0.43</td>
<td>0.40</td>
<td>0.17</td>
<td>-</td>
</tr>
<tr>
<td>Layer 1</td>
<td>1</td>
<td>0.38</td>
<td>0.36</td>
<td>0.28</td>
<td>-</td>
</tr>
<tr>
<td>Layer 1, trace 5</td>
<td>1</td>
<td>0.55</td>
<td>0.40</td>
<td>0.17</td>
<td>0.026</td>
</tr>
<tr>
<td>Layer 1</td>
<td>1</td>
<td>0.53</td>
<td>0.13</td>
<td>0.14</td>
<td>-</td>
</tr>
<tr>
<td>Layer 2</td>
<td>1</td>
<td>0.50</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Layer 2</td>
<td>1</td>
<td>0.52</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Layer 3</td>
<td>1</td>
<td>0.52</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

undulatory exterior of the carapace (relief 20–30 μm). The outer margin of Layer 1 is irregular, with a relief of 1–5 μm. The inner surface of Layer 1 has an irregular contact with the underlying carapace, with a relief of 1–2 μm.

Layer 2 is about 400 μm thick and consists of a layer of dense bone at the margin of the carapace (Fig. 5). Lacunae are present in Layer 2, but they are generally small (<20 μm in diameter) and separated by as much as 200 μm.

The innermost layer (Layer 3) is similar to Layer 2, but contains abundant large lacunae, as much as 150 μm in diameter, which are closely spaced (Fig. 5). Laterally, the size and spacing of lacunae varies considerably.

Nine EDS point analyses were made of UNM SB 42696, including six of the epidermal scale and three of Layers 2 and 3 (Table 3). The bone in Layers 2 and 3 showed a very consistent composition with a calcium:phosphorus ratio of 1:0.51 (n = 3). No other elements were detected. Layer 1 consists of a material rich in calcium and phosphorus with variable amounts of sulfur, silicon, and magnesium. Presumably compositional variation is related to the color pattern.

In overall micro-morphology, the carapaces of UNM SB 42696 and LACM 127773 are very similar. Each consists of an outer, thin epidermal layer which contains a color pattern, a medial layer of essentially dense bone, and an inner, more cancellous layer. However, the Neurankylus, cf. N. eximius, carapace is about twice as thick as that of the Pseudemys, and the color-bearing layer is relatively much thicker. In LACM 127773 the ratio of Layer 1 thickness to total thickness is 1:4.7, whereas in UNM SB 42696 it is 1:22. In both specimens the bone below the epidermal layer has a similar composition, being composed predominantly of calcium and phosphorus with a ratio in Neurankylus of 1:0.48 (n = 3) and in Pseudemys of 1:0.51 (n = 3). This is consistent with data indicating that fossil bone is composed of collophane, an altered form of apatite present in Recent bone.

There is a large difference in the composition of the color-bearing layers in the two specimens. In the extant tortoise, the epidermal layer appears to be composed of apatite and compounds rich in sulfur, silica, and, locally, magnesium. Therefore, the fossil tortoise would be expected to have a color-bearing layer composed of collophane with compounds rich in sulfur, silica, and magnesium. However, in LACM 127773, the color-bearing layer is composed of material rich in iron, calcium, silica, manganese, and aluminum. This compound is not a phosphate. By analogy with the Recent turtle, the calcium in Layer 1 is probably derived from hydroxyapatite. However, although iron and aluminum could be enriched by replacement of calcium in collophane (Rogers, 1924), phosphate would be expected to remain. Comparing the compositions in the two turtles, it is apparent that in LACM 127773 iron and manganese have been introduced into the color-bearing layer, and silicon and, locally, sulfur have been enriched.

Preliminary analysis of the color-bearing layer in LACM 127773 therefore suggests that the epidermal layer has suffered chemical alteration including the introduction of large amounts of iron and magnesium. This alteration has "fixed" the color pattern. The large amount of iron in the specimen suggests that alteration/diagenesis occurred in an anoxic environment. It is also important to note that the extensive diagenetic alteration of the color-bearing layer of LACM 127773 renders doubtful the notion that the original colors are preserved. The pattern of dashed lines on a light background almost certainly is the original color pattern. However, the reddish-brown colors (Fig. 3) argues that the reduction of the epidermal layer of large amounts of iron and manganese. The original colors were probably lighter.
COMPARISON OF THE COLOR PATTERN OF *NEURANKYLUS* WITH THE COLOR PATTERNS OF RECENT TURTLES

Spotted color patterns are relatively uncommon among living turtles. Many turtles have uniform colorations, radiating lines or streaks from a central blotch, reticulated patterns of congruent lines, simple stripes, or large blotches near the centers of major carapace scutes. Nearly all members of the Pseudemysiduridae have uniform carapace colorations, and only about 20% of cryptodiran turtles adequately illustrated by Wernmuth and Mertens (1961) and Pritchard (1979) have spotted patterns.

Of the extant turtles judged to have spotted color patterns, more than 50% are trionychids. These turtles have circular markings on the shell that are either solid spots or ocelli with the ground color inside a contrasting circular border. These spots vary in size from small punctuations to large juxtaposed markings that visually resemble a reticulation. Trionychid turtles lack epidermal scales but the spotted color pattern is directly associated with the epidermis.

Other extant spotted turtles include the emydids: *Clemmys beali*, *C. guttata*, *Emydoidea blandingii*, *Emys orbicularis*, and *Terrapene klauberi*. Of these taxa, only *Clemmys beali* has dark spots or punctuations on a light background (Boulenger, 1889) instead of the more common color pattern of light spots on a dark background. Other emydid turtles (e.g., *Terrapene carolina*) may have spotted color patterns in neonates and juveniles, but lose the spots as they grow. Some kinosternid turtles, especially *Claudius angustatus* and *Sterotherus minor*, have relatively light brown carapaces with dark spots or blotches. The spots are occasionally arranged in rows which coalesce in radiating streaks, but in some individuals the spots are scattered, forming a spotted pattern similar to the fossil color pattern seen in LACM 127773. Other kinosternids tend to be unicolored, or have dark streaks along the margins of scutes forming a dark reticulate pattern.

Other extant turtles with spotted patterns include a terrestrial testudinid *Homopus signatus* and the leatherback sea turtle *Dermochelys coriacea*. *Homopus signatus* is a terrestrial African tortoise and has about equal amounts of dark and light pigmentation on the carapace, whereas *Dermochelys coriacea* occurs in open and coastal marine waters and has a predominantly dark carapace with numerous light spots.

In brief, the color pattern consisting of numerous dark spots on a lighter ground color is most common among extant trionychid and kinosternid turtles. These turtles are widespread in a broad variety of aquatic habitats, including large rivers and streams with moderate currents and large permanent bodies of quiet waters with soft substrates of mud or sand (Pope, 1961; Webb, 1962). Several African, Southeast Asian, and North American trionychids attain large body sizes and primarily occupy benthic habitats in large rivers and lakes. The large size of *Neurankylus eximius* suggests that it too existed in large bodies of water. If the spotted pattern functioned in providing cryptic coloration, it would have been effective only in clear and moderately turbid water where the potential predators could effectively use vision to locate prey. The spotted pattern may function best in benthic turtles where the pattern blends with the color pattern of the substrate, although it may have been equally effective while basking on a bank.

CONCLUSIONS

The comparison of the color pattern of *Neurankylus* with that of extant turtles is consistent with sedimentological and osteological evidence that it was a benthic, aquatic turtle favoring large, standing bodies of fresh water.

The Paleocene occurrences of *Neurankylus* in the San Juan Basin are in silty/sandy mudstones of the Puercan and Tropicocan intervals of the Nacimiento Formation. Available sedimentological analysis of the Nacimiento Formation is not detailed, but does suggest extensive pond deposits represented by laterally persistent mudstones and siltstones (Balcz, 1967; Tsenta et al., 1981). Hutchison and Archibald (1986) noted a close association of selenomycodiran (including baenid) turtles with channel sandstones in the Upper Cretaceous–Paleocene of Montana. Shells of *Neurankylus*, however, are an exception to this association, being collected from mudstone and siltstone (Hutchison and Archibald, 1986). The facies association of *Neurankylus* specimens in New Mexico and Montana thus do not fit the usual channel-sandstone association of baenid turtles, and are suggestive of turtles that favored standing, not running, water.

Several osteological features of *Neurankylus* indicate that it was a bottom-dwelling, aquatic turtle. These include the large, heavily built, fusiform carapace, the large, recurved, terminal phalanges (documented on UNM NP-010), and the very long tail (Russell, 1935; Hutchison and Archibald, 1986). These features, together with the facies associations of *Neurankylus* fossils and the color pattern of *Neurankylus* documented here, combine to support strongly the notion of *Neurankylus* as a large, benthic turtle favoring standing bodies of water during the Late Cretaceous and Paleocene.

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