J. Paleont., 76(3), 2002, pp. 558–564

0022-3360/02/0076-558$03.00

MANUS-ONLY SAUROPOD TRACKS IN THE UHANGRI FORMATION (UPPER CRETACEOUS), KOREA AND THEIR PALEOBIOLOGICAL IMPLICATIONS

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ABSTRACT—One hundred and five sauropod tracks were excavated from black shale of the Uhangri Formation (upper Cretaceous), Haenam County, South Chulla Province, Korea. The tracks are true manus prints (not undertracks) and were made by sauropod dinosaurs while swimming.

INTRODUCTION

KOREA HAS yielded some of the world's most important dinosaur tracksites (Lockley, 1991). All tracks occur in the Gyeongsang Supergroup (Cretaceous). The Gyeongsang Supergroup outcrops in the large Gyeongsang Basin in southeastern Korea, and in several smaller basins (Haenam, Neungju, Jinan, Kyokpo, Yongdong, Kongju, and Eumsung) in the southwestern part of the Korean Peninsula (Fig. 1.1). These small basins are extensional basins formed in the overriding continental plate and frontal arc caused by oblique convergence and giving rise to strike-slip movement (Chun and Chough, 1992). In the Gyeongsang Basin the Gyeongsang Supergroup is divided into the Shindong and Hayang groups, mainly comprised of thick siliciclastic sequences of alluvial, fluvial, and lacustrine sediments, and the Yuchon Group, characterized by the dominance of volcanic rocks (Chang, 1975, Fig. 2). Tracks have been found frequently in the Shindong and Hayang groups (Lee et al., 2001). The best known tracksite is in the Dukmyeongri area, located in Goseong (Kosong) County, Gyeongsang Province (Yang, 1982; Lim, 1991; Lim et al., 1989, 1994). The dinosaur ichnocoenosis of the Jindong Formation (Albian), Goseong County represents the world's largest sample (more than 600 trackways) from a single formation (Lee et al., 2000). There are also two kinds of bird tracks, *Koreanaornis hamanensis* and *Jindongornipes kimi* (Kim, 1969; Lockley et al., 1992a).

In addition to the Dukmyeongri area, the Uhangri tracksite of Haenam County, South Chulla Province is of scientific importance because it is the only place in the world where dinosaur, pterosaur, and bird tracks all occur together (National Monument Designated Number 394, exact location on file at Cultural Properties Administration). The unnamed pterosaur tracks are the first reported from Asia (Huh et al., 1996; Lockley et al., 1997) and *Uhangrichnus chuni* and *Hwangsanipes choughi* are the oldest bird tracks with webbing traces (Yang et al., 1995). In 1997, excavation was carried out in the Uhangri area at three sites (I, II, III), using heavy equipment to cut into the sea cliffs. In the course of this work, pterosaur, bird, and dinosaur tracks were newly found at sites I and II, which are presently under investigation.

At site III, a total of 105 sauropod tracks were excavated in a 270 m^2 area of seaward-dipping (N60°W, 21°SW) black shale. The surface is smooth and virtually unbroken in most places. All tracks are circular in shape with no indication of claw impressions. Although some footprints are deep and others quite shallow, a common internal structure is present within each track. The purpose of this paper is to document these unusual tracks and to discuss their paleobiological implications.

GEOLOGICAL SETTING

The Haenam Basin is one of a series of isolated, NE-SW trending, Cretaceous non-marine basins distributed in Haenam County, South Chulla Province, southwestern Korea. It contains four formations, in ascending order: an andesitic tuff with andesite intrusions and flows, the Uhangri Formation, the Hwangsan Tuff, and the Jindo Rhyolite (Lee and Lee, 1976; Chun and Chough, 1995). The Uhangri Formation is an epiclastic sedimentary sequence (approximately 400 m thick) deposited in fluviolacustrine environments (Son et al., 1980). It comprises a thick sequence of conglomerate and gravelly sandstone, and overlying thin sequences of sandstone/cherty mudstone, crudely stratified sandstone, and black shale. It generally shows a fining-upward trend with four facies associations: alluvial fan fringe, subaqueous delta lobe, delta front, and shallow lake (Chun and Chough, 1995). The upper part of the Uhangri Formation is well exposed in the sea cliffs and intertidal wave-cut benches along the northern coast at Uhangri, Uhangpo, Sinsungri, Naesanri and Byongonri (Fig. 1.2). The Uhangri section (sites I, II, III) is comprised of laminated black shale and cherty mudstone alternating with stratified sandstone (Fig. 1.3). Symmetrical wave ripples in stratified sandstone, syneresis cracks, drifted small plant debris and various vertebrate tracks (dinosaurs, birds, pterosaurs) in black shale indicate that the water level remained rather low in the Uhangri area, suggesting a marginal lacustrine depositional environment (shallow lake facies). Invertebrate trace fossils such as *Planolites*, *Skolithos* and arthropod tracks also are observed occasionally on sandstone and mudstone surfaces.

The black shale containing dinosaur tracks (Uhangri section III) consists of silt-rich gray laminae alternating with mud-rich dark gray laminae. Each lamina is 0.1 to 2 mm in thickness and silt-rich laminae fine upward. Some lenticular siltstone is intercalated with fine sandstone laminae. Calcareous nodules, syneresis cracks, and pyrite framboids commonly occur in the black shale. No mud cracks occur, indicating that this area did not experience long subaerial exposure. Ostracodes of freshwater origin (*Candona* and *Ilyocypris*) have been recovered from some layers. High organic matter content (0.31 ~ 1.55 percent, average 0.75 percent; Son et al., 1980) and common framboidal pyrite in the black shale suggest that deposition occurred in a reducing environment with relatively high pH and silica concentration. This probably accounts for the low diversity of body and trace fossils at the site, other than dinosaur tracks and allochthonous plant remains.

The Hwangsan Tuff and andesitic tuff, which overlie and underlie the Uhangri Formation, respectively, were dated by $^{40}K/^{40}Ar$ at 82.8 ± 1.7 Ma and 94.1 ± 2 Ma (Moon et al., 1990). To refine the age of the tracks, whole rocks were collected and dated from two lapilli andesites 36 m below the track-bearing bed. The 83 ± 2.4 Ma $^{40}K/^{40}Ar$ date obtained represents the maximum age of the tracks.

TRACK DESCRIPTION

Although the 105 Uhangri tracks are variable with respect to depth and size, they appear to have been made by the same kind

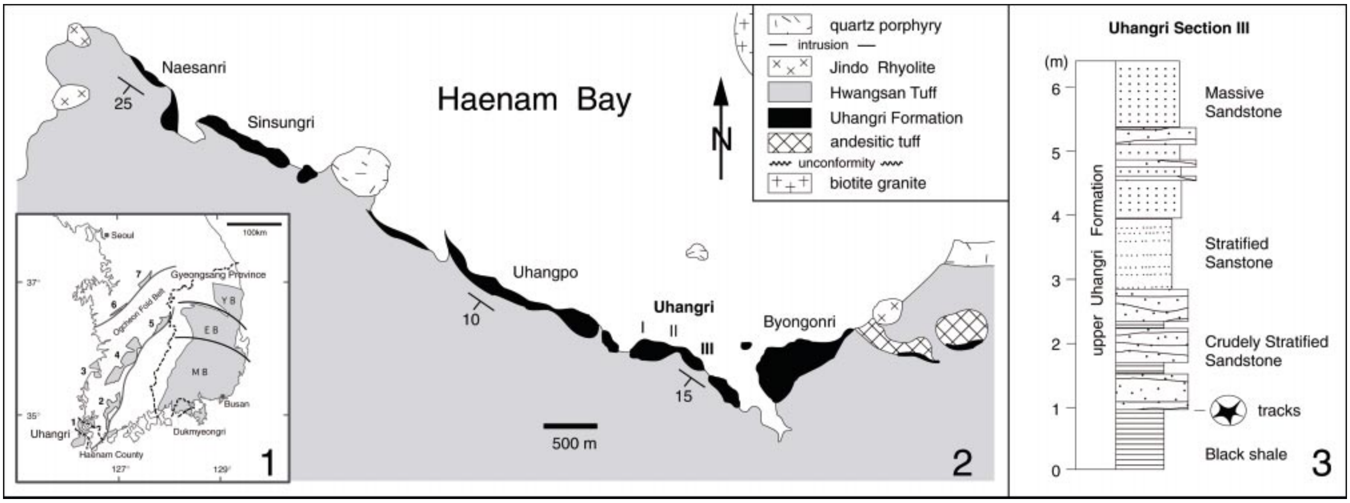

FIGURE *1—1*, Distribution of Cretaceous basins (shaded) and the Jurassic to Cretaceous fault pattern in the Korean Peninsula. Numbers indicate subordinate Cretaceous non-marine basins: 1, Haenam; 2, Neungju; 3, Kyokpo; 4, Jinan; 5, Youngdong; 6, Kongju; and 7, Eumsung basins. *2*, Simplified geological map of the study area (modified from Chun and Chough, 1995). *3*, Stratigraphic section of the Uhangri Formation showing track-bearing horizon at Uhangri site III. Abbreviations: YB, Yeongyang Block; EB, Euiseong Block; MB, Milyang Block.

of animal because they form trackways. The outlines of tracks are circular in shape, ranging from 71 to 77.6 cm in diameter (90 percent of the tracks). All tracks are large basin-like depressions, not surrounded by a raised rim (bourrelet) of displaced sediment (Fig. 3). They are gently dipped into the center from the bedding plane, without vertical margins. The laminae of black shale are not punctured but are continuous beneath the tracks. Thus, the tracks are similar to what would result from impressing finger tips slowly into elastic clay. A shallow region is present in the center of each impression, with ridges radiating towards the outer margins. Although the widths and heights of these ridges are not consistent, they generally taper and decrease from the center outward, respectively. The ridges are less than five in number, and never rise above the level of the bedding plane. The angles between the ridges vary in the tracks so that it is not possible to identify a consistent arrangement of ridges.

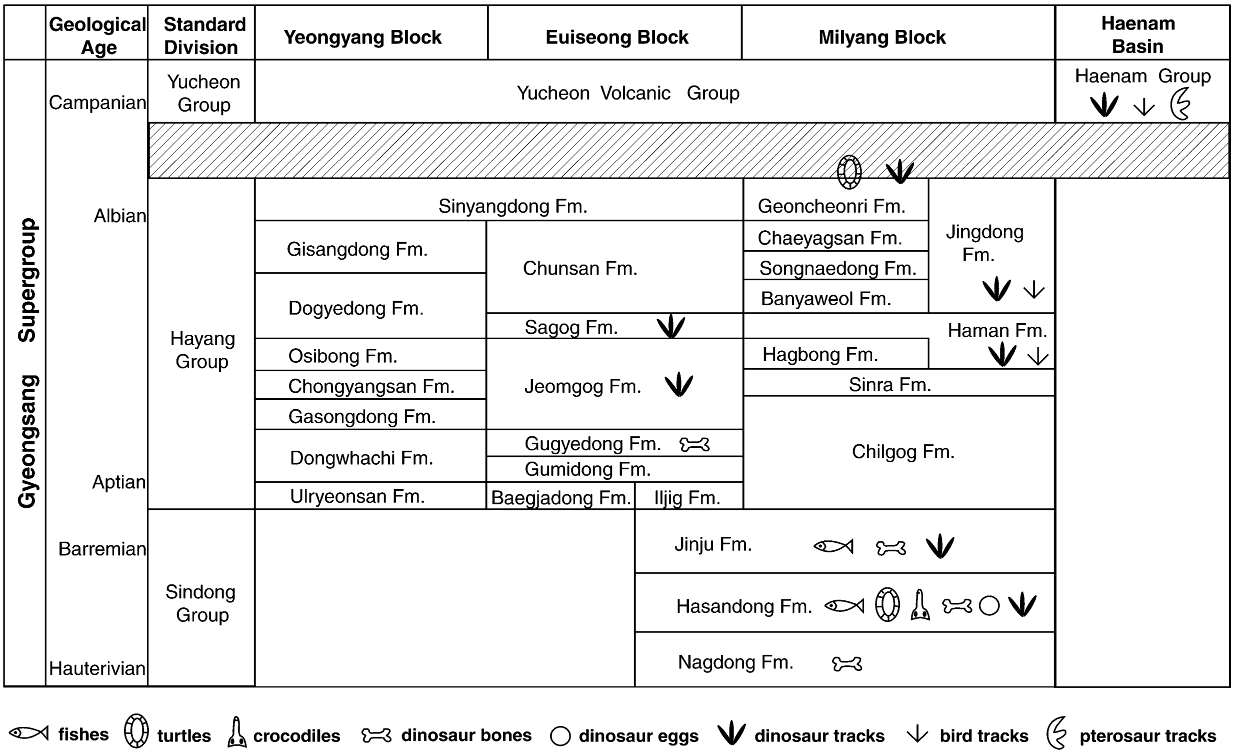

FIGURE *2*—Stratigraphic correlation of the Gyeongsang Supergroup and the Haenam Basin with the vertebrate faunal horizons. Geological ages are based on palynomorphs (Choi, 1985, 1989; Yi et al., 1993, 1994; Y.-N. Lee et al., 2000) and paleomagnetism (Moon et al., 1990; Doh and Kim, 1994).

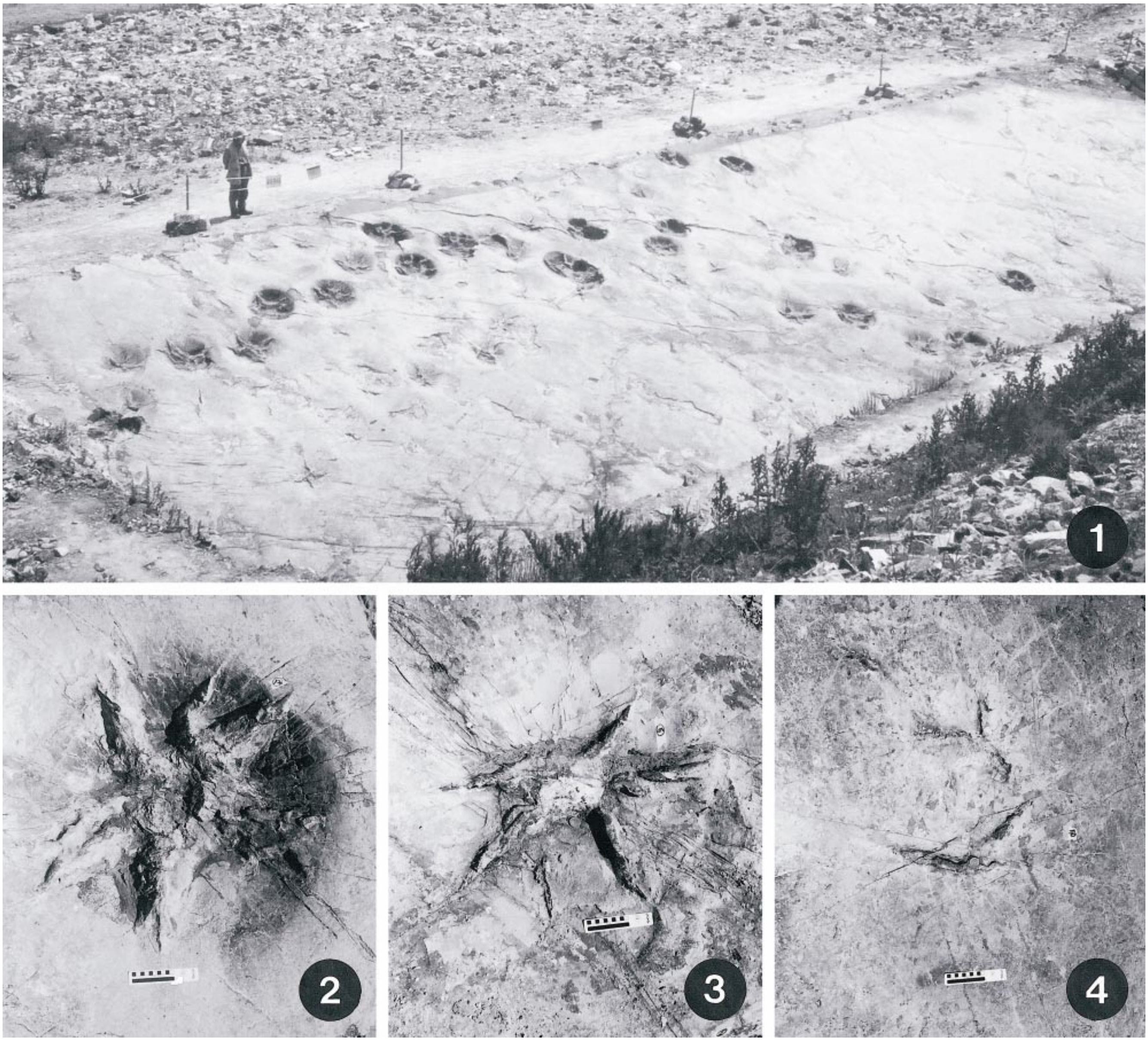

FIGURE 3—*1,* Trackways in the Uhangri Formation at Uhangri site III. *2,* Track number 12 (Group 1). *3,* Track number 5 (Group 2). *4,* Track number 50 (Group 3). Scale = 10 cm.

All tracks can be divided into three groups by the depth and the definition (or sharpness) of outlines (Fig. 4). The deepest 32 tracks (average 16.4 cm in depth) are well defined by sharp circular outer margins (Group 1, Fig. 3.2). The ends of the ridges always touch the outer margin. The second group (Group 2–30 tracks, average 9.32 cm in depth) has the same internal structure as the first group, but the ridges are thinner than those of Group 1, not reaching the outer margins (Fig. 3.3). The third group (Group 3–43 tracks) consists of tracks that are shallowly impressed (average 5.2 cm) and have ridges irregular in shape and length (Fig. 3.4).

The high density and considerable depth range of the tracks make trackways difficult to identify, and suggest that all trackways were not made at the same time. This conclusion is supported by several superimposed prints and cross trackways. The trackways have two major orientations (north-south and east-west), but it is difficult to trace complete trackways due to lack of consecutive footprints. In addition, the pace and pace angulation is not constant in most trackways. The depth of footprints also is variable in a single trackway, comprising different groups. Nevertheless, two sets of consecutive tracks [trackway 1: track number 8, 9, 10, 12, 14, 15, 17, 20(?) and trackway 2: track number 34(?), 51, 41, 52, 53, 68(?)] could be identified as segments of trackways based on their consistent stride and pace angulation (Fig. 5). Because there is no indication of foot orientation in these prints, it is impossible to determine the direction of travel. The average minimum and maximum diameters are consistent in trackway 1 (76.8 cm and 82.7 cm) and trackway 2 (73 cm and 82.7 cm). However, the pace and stride length of trackway 2 (126 cm and 244 cm, respectively) are bigger than those of trackway 1 (115 cm and 202 cm). The pace angulation is larger in trackway 2 (136.5 degrees) than in trackway 1 (127.8 degrees) as well. Thus, the maker of trackway 2 appears to have moved faster than the maker of trackway 1.

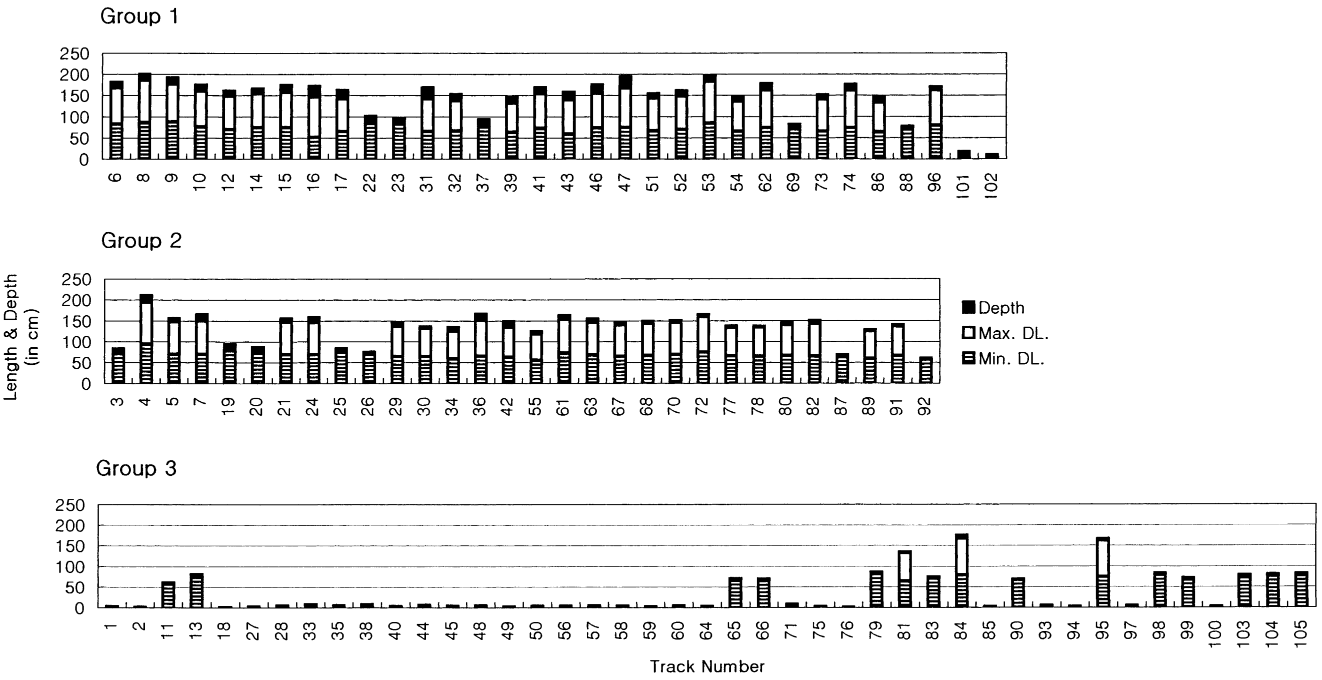

FIGURE 4—Histograms of Uhangri sauropod manus tracks by groups. Abbreviations: Min. L, minimum diameter length; Max. L, maximum diameter length; Depth, footprint depth.

TRACK INTERPRETATION

The internal structures within these tracks are interpreted as extrusion of the lower water-saturated mud upward through the overlying, elastic yet firm layers, by means of fractures generated by the impact of a dinosaur's foot. They are not sediment fills deposited into the tracks, because the ridges consist of the same material as the substrate. It is not likely that the ridges were made by bulging up of the substrate between the track-maker's toes. The size of the ridges is directly proportional to the depth of the tracks, indicating that the greater downward force produced the more prominent ridges. With the inconsistency in arrangement of ridges, the internal configuration of the track represents a typical cracked-open pattern in which the ridges taper from the center outward. This pattern possibly could be further distorted by a suction effect, as reported for ornithopod footprints in the Woodbine Formation, Texas (Lee, 1997). The floor of the print tends to be drawn upwards as the animal withdrew its foot from wet and sticky sediments. If that is true, these tracks are not underprints but true prints that the trackmakers made on the mud surface. This conclusion is reinforced by the absence of footprints in the overlying crudely stratified greenish sandstone observable in vertical columnar sections of the excavated site III. In addition, the surface of the tracks does not include sand grains that should have been left had the animal pushed the sandy upper layer into the muddy underlayers.

Sauropod dinosaurs were habitual quadrupeds (Thulborn, 1989). Well-preserved manus prints generally have a semi-circular or horseshoe shape. The best known sauropod ichnospecies, *Brontopodus birdi* from the Glen Rose Formation of Texas, has a "double crescent" shaped manus print, suggesting relatively little development of a fibrous pad behind the metacarpals (Farlow et al., 1989). This morphology is observed in the sauropod trackways from the Middle Jurassic Galinha site, Portugal (Santos et al., 1994, fig. 3), and a well-preserved track set, TMM 40637-1, from the Early Cretaceous West Verde Creek site excavated by R. T. Bird in 1940 (Pittman, 1989, fig. 15.12). The circular impressions also are common in sauropod manus tracks, as in the manus-dominanted trackways from the Middle Jurassic beds of Morocco (Ishigaki, 1989, fig. 9.2), and a sauropod trackway in the Jindong Formation (Albian) of Korea (Lee et al., 2000, fig. 6). In addition, the continuously sloping surfaces around the circular footprint clearly indicate that the track was made by a round foot. Therefore, it is unlikely that these rounded Uhangri tracks were made by ornithopod dinosaurs with tridactyl morphology. Ornithopod pes prints are nearly always tridactyl with three stout and broadly spreading toes so that the resulting footprint has the outline of a trefoil (Thulborn, 1990, p. 190).

In general, footprints can be imprecise representations of foot skeletons, especially those associated with ample soft tissues on the foot. Nevertheless, some tracks may reflect the foot structure of their trackmakers with fidelity. Manus prints of *Brontopodus birdi* and TMM 40637-1 have a morphology consistent with the manus structure of *Brachiosaurus brancai* (HMN SII, Janensch, 1961) and *Janenschia robusta* (HMN Nr. 5, Janensch, 1961), in which long and slender metacarpals are held in a vertically oriented tubular or semi-circular arrangement, a synapomorphy for Neosauropoda (Upchurch, 1994; Wilson and Sereno, 1998). Distally, the metacarpals diverge slightly, leaving manus prints with metacarpals II–IV bound together into a digital pad ("crescent" shape) somewhat separate from metacarpals I and V, as in *Brontopodus birdi* (Farlow et al., 1989) and TMM 40637–1 specimen (Pittman, 1989). *Breviparopus taghaloutensis* (Dutuit and Ouazzou, 1980) may have had metacarpals I and V more tightly connected to the central metacarpals. The Uhangri tracks also reflect the anatomical features of the trackmaker's manus. They suggest that Uhangri sauropods had a digitigrade stance with a circularly arranged tubular metacarpus. Each digit probably was separated, rather than bound together to form a mitten. There is no indication of claws on manus tracks.

The sauropod manus is characterized by phalangeal reduction

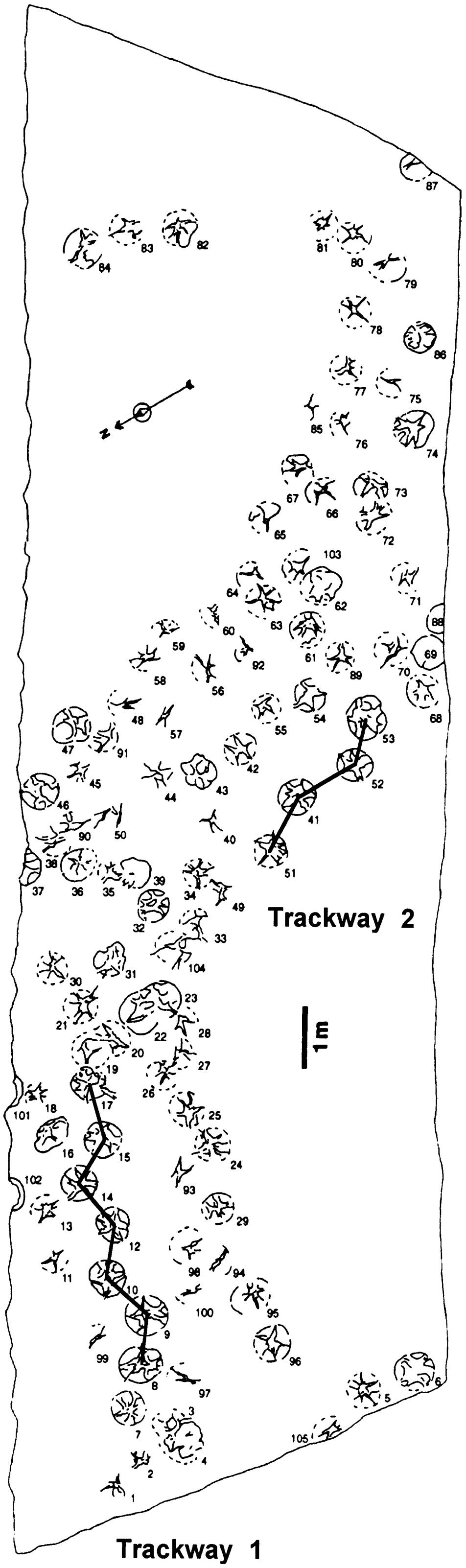

FIGURE 5—Map showing the distribution of tracks in the Uhangri Formation, Uhangri site III, Haenam County, South Chulla Province.

on digits II–IV and a claw on digit I (Upchurch, 1994). However, a claw mark on digit I is uncommon in sauropod tracks (Langston, 1974; Dutuit and Ouazzou, 1980; Jenny and Jossen, 1982; Ishigaki, 1989; Pittman, 1989; Farlow et al., 1989, fig. 42.8j) perhaps because sauropods may have carried the pollex claw above the ground by dorso–medial hyperextension (Thulborn, 1989). However, no claw mark is observed in deeply and evenly impressed Uhangri tracks compared with some sauropod manus tracks with claw marks (Ginsburg et al., 1966; Lockley et al., 1986; Santos et al., 1994). Among titanosauriforms (Wilson and Sereno, 1998), the claw of digit I is small in *Brachiosaurus* and *Pleurocoelus* (possibly the *Brontopodus*-maker), and absent in titanosaurs (Salgado et al., 1997). This suggests that the Uhangri manus tracks were made by titanosauriforms, in which the claw was probably either small or completely lost altogether.

Compared with circular manus prints, well-preserved sauropod pes prints usually have claw marks that are more laterally than anteriorly directed, with a somewhat U-shaped configuration. They are considerably longer than broad and outwardly rotated approximately 20–30 degrees. The medial side of prints is longer and deeper than the lateral side (Farlow, 1987). The ‘‘heel’’ of the pes print is distinctive, as shown in *Brontopodus birdi*, which was probably impressed by a thick pad of fibrous tissue that supported the rear of the foot (Norman, 1985). Such typical pes prints are not found in the Uhangri study area. Sauropod footprints show heteropody, with relatively small manus and large pes prints. The manus and pes area ratios range between 1:1.2 (Lee et al., 2000, fig. 6), 1:2 (Santos et al., 1994), 1:3 (*Brontopodus birdi*, Bird, 1941), and 1:5 (*Parabrontopodus mcintoshi*, Lockley et al., 1994a). If the manus/pes ratios above are applied to the Uhangri prints, pes prints would be predicted to reach at least 1 m long at the site. No prints of such size or morphology have been found, however, and therefore, there appear to be manus-only sauropod tracks at Uhangri.

DISCUSSION

Sauropod trackways dominated by manus impressions are quite common around the world. They are known from the Middle Jurassic beds of Morocco and Portugal (Ishigaki, 1989; Santos et al., 1994), the Upper Jurassic beds of Portugal (Lockley et al., 1992b, 1994b; Lockley and Santos, 1993), and the Lower Cretaceous Glen Rose Formation, Texas (Bird, 1944, 1985; Pittman, 1989; Lockley et al., 1994c). Manus dominant trackways are divided into two patterns by their occurrences (sensu Lockley et al., 1994c). One pattern comprises shallow manus-dominanted trackways on smooth surfaces, regarded as underprints transmitted through thin beds to firm underlayers. It is notable that such undertracks are always shallowly impressed and vaguely defined with unclear margins. The second pattern consists of incomplete manus-dominated or manus-only trackways associated with more irregular, burrowed surfaces. In this case, tracks are all relatively deep with clear vertical margins, as seen in the Portlandian beds at Lagosteiros Bay, Portugal (Santos et al., 1994, fig. 7). The substrate condition of the Uhangri tracks is similar to the former category, in that tracks occur on smooth surfaces without invertebrate bioturbation. The Uhangri tracks, however, are not underprints but true manus impressions, a situation clearly different from the first category. This evidence indicates that manus-dominant trackways are not always undertracks. With regard to depth, the Uhangri tracks could be assigned to the second category, but their occurrences, the substrate condition, and the shape of track margins are quite different.

The manus-dominanted trackways initially were interpreted as having been made by swimming animals that floated their hindquarters while walking along the bottom with their forelimbs (Bird, 1944, 1985; Coombs, 1975; Ishigaki, 1989; Thulborn,

FIGURE 6—Reconstruction of a floating sauropod conjectured from the Uhangri sauropod manus tracks. Skeletal silhouette is based on *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977; Wilson and Sereno, 1998).

1990; Czerkas and Czerkas, 1990; Norman, 1991). This explanation has been challenged recently by the new interpretation that they are undertracks and, therefore, not attributable to the activity of a partly buoyant animal (Lockley and Rice, 1990; Lockley, 1991). Some sauropod dinosaurs had extreme heteropody so that much greater downward force per unit area caused the front feet to sink in deeper on yielding substrates, which thereby increased the probability of leaving undertracks. In other words, the phenomenon is controlled by preservational factors, rather than by the behavior of the trackmakers (Lockley et al., 1994c). However, such would not be the case if a greater proportion of weight was borne by the hind limbs as in sauropod tracks in the Broome Sandstone (Lower Cretaceous) of Western Australia (Thulborn et al., 1994). The prints described herein are clearly not underprints, but true manus prints of sauropods. The lack of trackway continuity, variations in the depth and stride of the footprints in a single trackway, and the occurrence of isolated tracks indicate that the animals did not walk with normal gaits. All evidence from trackways is suggestive of swimming animals moving along a muddy bottom, propelled by the manus (Fig. 6). Extra buoyancy probably made large sauropod dinosaurs change the gait sequence and the timing of limb movement. Therefore, the Uhangri manus tracks strongly support Bird's (1944) theory of sauropod swimming ability. Even if R. T. Bird was correct, it is not necessary to revive the ''aquatic sauropod'' hypothesis (contra Lockley and Conrad, 1989), because it does not mean that sauropods were always in a watery habitat. Swimming ability of dinosaurs is known from a bipedal theropod (*Anchisauripus*) in the Lower Jurassic rocks at Rocky Hill, Connecticut (Coombs, 1980), and a quadrupedal ornithischian dinosaur in the Cretaceous Dakota Formation, Kansas (McAllister, 1989). Ripple marks, shrinkage cracks and other current indicators ubiquitous in the Uhangri Formation (sites I, II) are absent totally from the bedding plane containing these footprints (site III). This indicates that relatively quiet water was standing over mud beds sufficiently cohesive to retain tracks. Additionally, the exclusive occurrence of these large footprints possibly implies that water was too deep for small animals to reach the bottom (Currie, 1983). The lacustrine mud in the region suggests that the sauropods entered the water intentionally and were not trapped by a sudden flood.

The Uhangri sauropod ichnites are the first Late Cretaceous manus-only sauropod trackways and are among the few Late Cretaceous sauropod tracks. Two sauropod tracksites previously known from Turonian deposits in Croatia (Gogala, 1975) and the Maastrichtian of Bolivia (Leonardi, 1984, 1989) are both ''wide-gauge'' trackways (sensu Farlow, 1992). The Uhangri ichnites demonstrate ''narrow-gauge'' trackways, which are less common in the Cretaceous than in Jurassic sediments (Lockley et al., 1994d). It is, however, not certain whether the ''narrow-gauge'' configuration of Uhangri tracks reflects taxonomy or locomotion under the water. Therefore, taxonomic designation based on only manus prints would be premature without associated pes impressions.

ACKNOWLEDGMENTS

We wish particularly to thank J. O. Farlow (Indiana-Purdue University) for his critical review of our earlier version of the manuscript and useful comments. We are grateful to two anonymous referees for their helpful comments. For the excavation, we are deeply indebted to S.-K. Lim (Kyungpook National University) and students from Chonnam National University and Kyungpook National University. Acknowledgment is made to the special fund for the ''Uhangri Dinosaur Center and Theme Park,'' administered by Haenam County and South Chulla Province, for the full support of this research. This work is also partially supported by BK21 project of Korea to the senior author.

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ACCEPTED 25 JUNE 2001