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A SAUROPOD TRACKWAY IN DONGHAE-MYEON, GOSEONG COUNTY, SOUTH GYEONGSANG PROVINCE, KOREA AND ITS PALEOBIOLOGICAL IMPLICATIONS OF UHANGRI MANUS-ONLY SAUROPOD TRACKS

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Abstract: Sauropod tracks at Jageun Guhakpo tracksite consist of 11 consecutive footprints comprising a trackway of about 8 meters. The average manus length and width is 64.4 cm and 67.0 cm, respectively. These tracks are broadly rounded shaped without claw mark in digit I. Digit V has slightly larger area than digit I and there is no separating for digits II-IV impressions. The average pes length and width is 112.3 cm and 95 cm, respectively which is the largest pes print in Korea. The inner trackway width clearly indicates a 'narrow gauge' pattern. A sauropod dinosaur belonging to the Diplodocidea or the Macronaria can be suggested as a candidate for the Jageun Guhakpo trackmaker based on skeletal and ichnological synapomorphies, animal size, and provenance. Jageun Guhakpo sauropod tracks support that Uhangri sauropod tracks are manus true prints made by sauropod dinosaurs that floated their hindquarters while walking along the bottom with their forelimbs. The floor of each print is raised into a starburst pattern of crests radiating from the center towards the outer margin, making an extraordinary morphology. The origin of this complex system of crests and intervening pockets were made as extrusion of thelower water-saturated mud upward through the overlying, elastic yet firm layers, by means of fractures generated by the impact of a dinosaur's foot. It is proved by crests comprising of coarser lower layer than finer surface layer and fine vertical striations observed on the walls of crests. Therefore, the extra-morphological features of Uhangri sauropod manus tracks can be much more reasonably explained by "cracked-open" model rather than "canopy" model recently proposed.

Key words: Sauropod tracks, Jageun Guhakpo, Goseong, Uhangri, Swimming

INTRODUCTION

Dinosaur footprints in Korea were first reported from the Cretaceous Jindong Formation (Albian) in the Dukmyeong-ri area of Goseong County in 1982 (Yang, 1982). Since then, new discoveries of dinosaur tracksites have been made in Goseong County (Lim *et al*., 1989; Lim, 1991; Yang and Lim, 1991; Lockley *et al*., 1993; Lim *et al*., 1994; Baek and Seo, 1998). Along with dinosaur tracks, abundant bird tracks were also found in the same region including bird ichnotaxa, *Jindongornipes kimi*, *Koreanaornis hamanensis*, and some on the same bedding plane as dinosaur footprints (Yang *et al*., 1990; Lockley *et al*., 1992b). In 2000, a comprehensive exploration for vertebrate ichnosites of Goseong County was performed by the Paleontological Society of Korea (Paleontological Society of Korea and Goseong County, 2000). As a result of this systematic reconnaissance, multiple dinosaur track-bearing levels were found in eight of all fourteen districts of Goseong County. Although some dinosaur tracks are also found in road cuts, quarries, and stream beds, abundant dinosaur tracks occur mainly in extensive coastal exposures in Hai, Donghae, and Hoehwa districts.

Approximately 410 dinosaur trackways and 4000 footprints were mapped from the Jindong Formation, representing the world's largest dinosaur ichno-sample from a single formation (Lee *et al*., 2000). Ornithopod trackways (249 in number) are the most abundant (61%), and show a strong tendency (maximum of 18 trackways) toward parallel orientation, implying gregarious behavior. Most footprints range from 25 cm to 45 cm in length, representing sub-adults or adults. Twenty-two trackways (5%) are attributed to theropods, which were not traveling together in herds. A total of 139 trackways (34%) are of sauropod origin. Although they indicate social behavior (herding), sauropods were not as gregarious as ornithopods in terms of herd size and consistency of trackways in parallel orientation. These sauropod tracks were made mostly by small, juvenile or sub-adult size classes, but one trackway in Jageun Guhakpo of Donghae District consists of the largest sauropod footprints in Korea.

The purpose of this paper is to describe the Jageun Guhakpo sauropod trackway and to infer the track-maker from its footprint morphology, and finally to investigate the paleobiological implications of manus-only sauropod tracks in Uhang-ri, Haenam County, South Jeolla Province.

GEOLOGICAL AND SEDIMENTOLOGICAL SETTING

The Jindong Formation is dominantly distributed in Goseong County and especially well exposed in coastal cliffs in Hai, Hail, Donghae, and Hoehwa districts. The Jindong Formation (more than 1500 m thick) consists predominantly of dark gray calcareous mudstones, siltstones, and fine sandstones of lacustrine origin. Mud cracks and small-scale ripples occur repeatedly in thin laminated horizons which indicate shallow lacustrine and lake margin environment. Calcrete-intraclast pebble conglomerate and pedogenic carbonate are sometimes interbedded with mudstones and sandstones. Most dinosaur tracks are preserved in fine sandstones and siltstones-mudstones deposited on a dry mudflat at the lake margin.

Except for trace fossils, both body fossils of fauna and flora are extremely rare throughout the formation, although very small gastropod, ostracode, and charophyte remains occur in some units. A quantitative analysis of palynomorph grains shows the significant dominance of gymnospermous pollen, such as *Corollina* (40.09%), *Inaperturopollenites* (19.79%), and *Perinopollenites* (19.27%). The presence of *Retimonocolpites* and *Tricolpites* is also noticed. These characteristic angiospermous taxa indicate an Albian age for the Jindong Formation. The composition of the microfloral assemblage indicates the vegetation of a warm and arid climate (Paleontological Society of Korea and Goseong County, 2000). Very high density of preservation of dinosaur footprints in the Jindong Formation is interpreted as the result of repeated deposition by sheet floods on a mudflat associated with a perennial lake, which was utilized by dinosaurs as a persistent water source during drought (Paik *et al*., 2001).

The sauropod trackway discussed here is located in costal outcrops at Jageun Guhakpo, Jangjwa-ri, Donghae District, Goseong County (Coordinates 34°59'26.37", 128°27'33.75")(Fig. 1). Donghae District is the second largest dinosaur tracksite in Goseong County. At least 1300 dinosaur footprints were reported previously from 163 track levels in 6 localities (Baek and Seo, 1998). Bird footprints (*Jindongornipes kimi*) were also found in this region. Jageun Guhakpo tracksite is located in the upper part of the Jindong Formation. Outcrops are exposed along the coastal cliffs up to 7 m above sea level so that surfaces large enough to recognize footprints are very limited, with the notable exception of one track-bearing horizon. The track-bearing horizon comprises a surface of about 50 m^2 that includes one sauropod trackway which consists of 11 consecutive footprints, though three tracks are incomplete. Except for dinosaur footprints, other trace fossils are not observed on the surface. Sauropod tracks are found on a mud-cracked surface, which indicates the walked on a dry mudflat at the lake margin. When the tracks were made on the mud-cracked surface, the mudflat was not completely dry and consequently strong walking downward force of the gigantic sauropod dinosaur drove its feet into the substrate, at the same time making a raised rim encircling each foot on the surface. The inside of some tracks shows a light grey calcareous mud underlayer (Fig. 2).

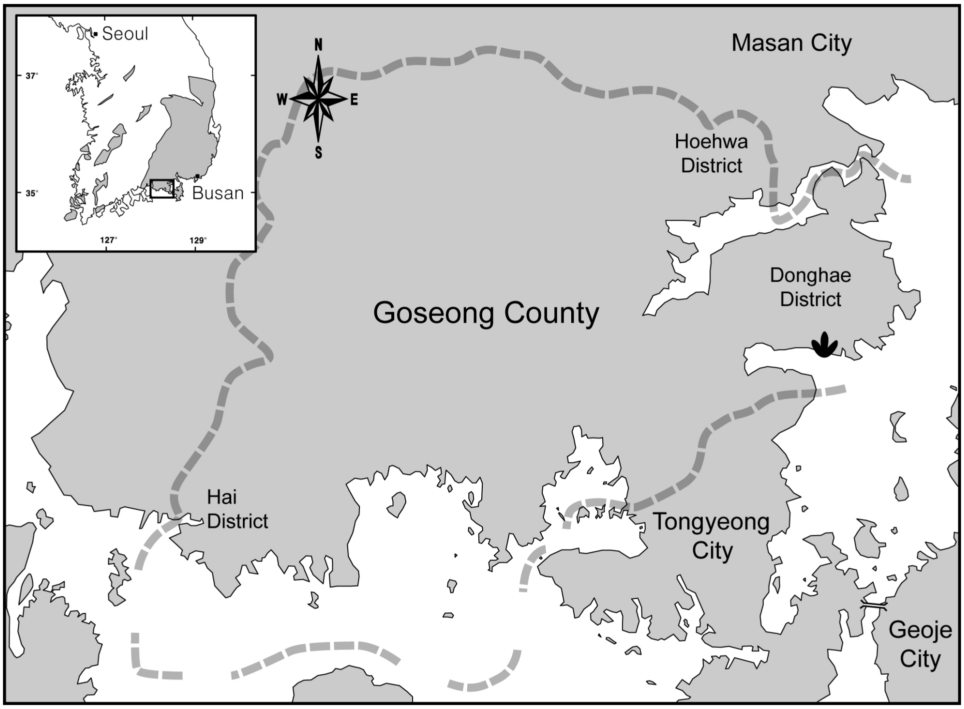

Fig. 1. Distribution of Cretaceous basins (shaded) in the Korean Peninsula and location of Jageun Guhakpo tracksite in Donghae District of Goseong County, South Gyeongsang Province (♣).

JAGEUN GUHAGPO SAUROPOD TRACKWAY

Jageun Guhakpo sauropod trackway was mapped and measured in the field. An accurate outline of each footprint was drawn directly a transparent vinyl sheet large enough to cover the whole trackway (Fig. 3). Photographs of each footprint were taken perpendicularly to the bedding plane to reduce optical distortion during study and illustration. Footprint and trackway parameters were measured on the outcrop: footprint length, footprint width, stride length, pace length, trackway width, footprint angulation, and pace angulation (Table 1).

Jageun Guhakpo sauropod trackway comprises 11 footprints in a trackway of about 8 meters length (Fig. 4). The trackway shows a quadrupedal gait pattern comprising manus and pes prints easily recognized by the distinctive print morphology. Six manus and five pes prints are observed in the trackway and each one is encircled by a raised rim of displaced sediment. The shape of each footprint is remarkably uniform, with subrounded bowl-shaped manus impressions and larger oval-shaped pes impressions. The average manus length and width are 64.4 cm and 67.0 cm, respectively. The manus print is slightly more than one-half the area of pes track, broadly round in shape, and with a distinct but not strong indentation of the middle of the posterior margin. There is no claw mark in digit I, which has a small and rounded impression. Digit V has slightly larger area than digit I. There is no separation of the digits II-IV impressions from I and V. All manus prints are oriented anterolaterally in relation to the direction of travel, with outward rotation of 37.9 degrees on average. The average stride length is 281.8cm and average pace length is 207.2 cm. The pace angulation is 105.5 degrees, and the inner trackway width is 34.6 cm, suggesting a clear 'narrow gauge' pattern. The average pes length and width are 112.3 cm and 95 cm, respectively, making these are largest pes prints in Korea. Pes prints are oval to subtriangular in shape, and

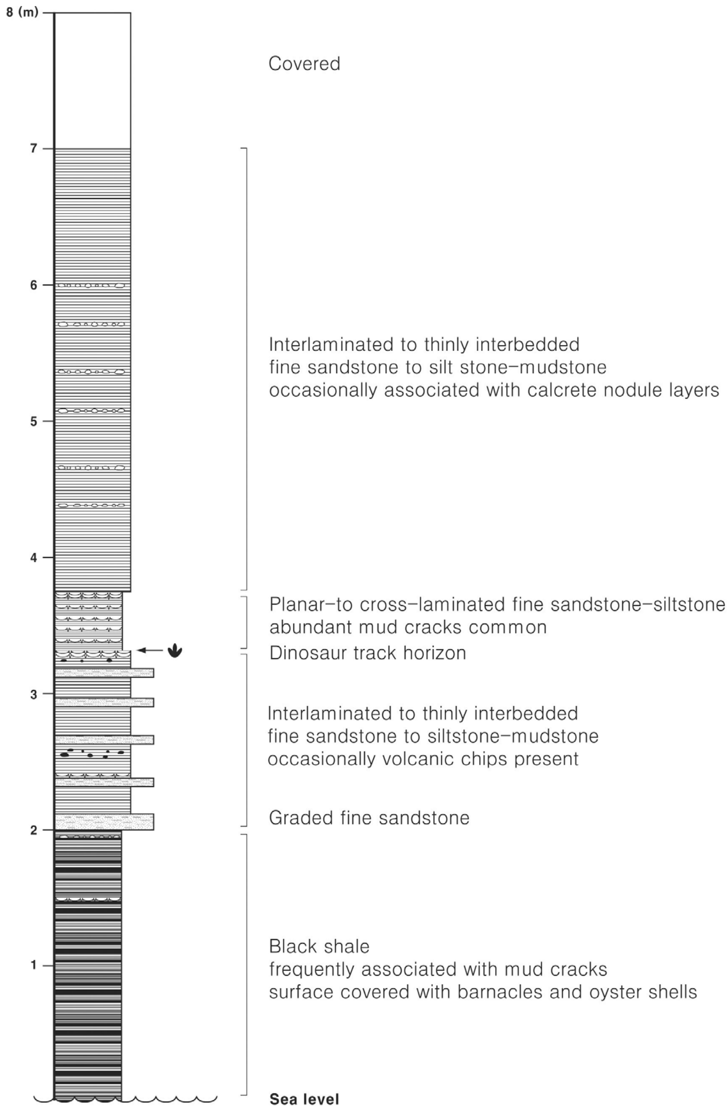

Fig. 2. Stratigraphic section of Jageun Guhakpo tracksite shown in Figure 1.

Fig. 3. Mapping and measuring directly on the field using a large transparent vinyl sheet enough to cover the whole trackway.

Table 1. Measurements from Jageun Guhakpo sauropod trackway, with terminology from Thulborn (1990). P/M; pes/manus; L/R, left/right; FL; footprint length; FW, footprint width; PL, pace length; SL, stride length; TW, trackway width; R, rotation angle; ANG, pace angulation.

NUMBER	P/M	L/R	FL	FW	PL	SL	TW	RA	ANG
LM1	M	L	67	63	?	?		21.8	
RM1	M	R	?	66	188	?	49	46.7	98
LP1	P	L	107	103	?	?		38.7	
RP1	P	R	106	97	178	?	0	42.5	111
LM2	M	L	68	67	236	280	39	30.9	109
RM2	M	R	60	67	192	286	30	48.3	108
LP2	P	L	124	90	193	263	-13	35	118
RP2	P	R	?	90	163	296	-15	36.6	117
LM3	M	L	69	67	219	280	25	39	107
RM3	M	R	58	72	201	281	30	41.1	
LP3	P	L	?	?	?	290			
AVERAGE	M		64.4	67	207.2	281.8	34.6	38	105.5
	P		112.3	95	178	283	-9.3	38.2	115.3

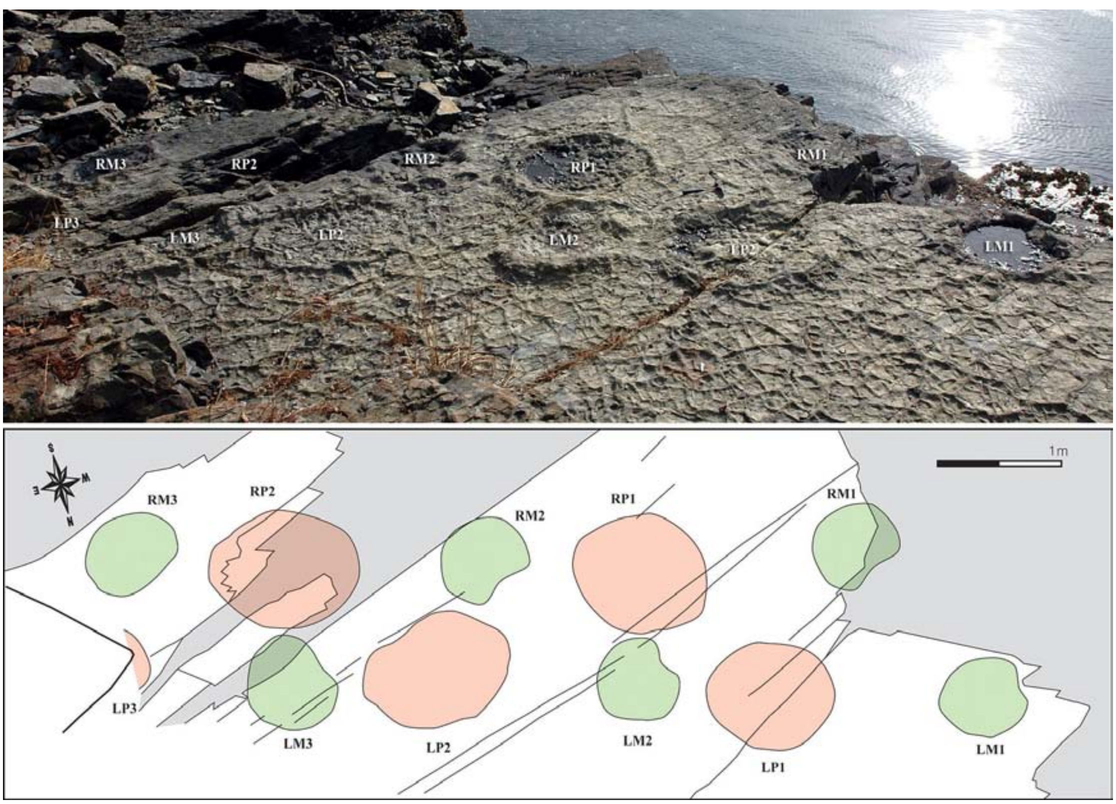

Fig. 4. Complete manus-pes sauropod trackway from Jageun Guhakpo tracksite. A, photograph. B, line drawing.

entire outlines can be seen clearly in most pes tracks, although details of claw marks are not evident. All pes prints are oriented anterolaterally in relation to the direction of travel, rotating outward 38.2 degrees on average. The average stride length is 283.0 cm and average pace length is 178.0 cm. The pace angulation is 115.3 degrees, and the inner trackway width is -9.3 cm showing a clear 'narrow gauge' pattern as in manus prints.

TRACKMAKER

The trackway is of *Parabrontopodus*-type, a narrow trackway characterized by no space between inner margins of left and right pes prints and strong outward rotation of manus and pes tracks. These tracks do not show the pronounced heteropody (manus:pes ratios of about 1:4 or 1:5) seen in *Parabrontopodus mcintoshi* (Lockley *et al*., 1994a). A clear eastward (S80°E) walking direction of the trackmaker can be recognized. The taxonomic identification of the trackmaker depends on the diagnostic features preserved in the trackway integrated with skeletal data (Olsen, 1995; Carrano and Wilson, 2001). It is difficult to identify pedal synapomorphies in the preserved pes tracks, which do not show details of pedal ungual morphology. However, the U-shaped manus print is a derived ichnological feature (synapomorphy) of the Neosaurpoda, which has articulated metacarpals that form a 270° U-shaped arc in proximal view (Gauthier, 1986; Wilson and Sereno, 1998; Wilson and Carrano, 1999; Sereno, 1999). Among the Neosauropoda, Titanosauriforemes can be excluded as a candidate of trackmaker because they have wide-gauge tracks due to a femoral shaft whose proximal one-third is deflected medially (Wilson and Carrano, 1999). Therefore, the Jageun Guhakpo trackmaker cannot have been a brachiosaurid or a titanosaurid. A neosauropod dinosaur as a candidate for Jageun Guhakpo trackmaker does not come into conflict with skeletal synapomorphies, animal size, and provenance. The large size of the Jageun Guhakpo trackmaker is within the range of Neosauropoda, which includes some of the largest sauropods, such as *Seismosaurus halli* (Gillette, 1991) and *Supersaurus vivianae* (Jensen, 1985). Neosauropods are also found in Asia, Europe, America, and Africa from the Middle Jurassic to Late Cretaceous.

Although not in the Jindong Formation, some sauropod skeletal materials have been discovered in the Gyeongsang Supergroup. These are isolated teeth and incomplete or fragmentary bones. A proximal portion of a left humerus found in the Gugyedong Formation at Tab-ri, Geumseong-myeon, Euiseong County is indeterminate taxonomically (Lee *et al*., 1997), and a new euhelopodid *Pukyongosaurus millenniumi* from the Hasandong Formation at an island of Galsa-ri, Geumseong-myeon, Hadong County (Dong *et al*., 2001) is now considered a *nomen dubium* (Upchurch *et al*., 2004).

Five isolated sauropod teeth are recognized in the Hasandong Formation: a euhelopodid, a camarasaurid, and three titanosaurid teeth (Lee *et al*., 1997; Park *et al*., 2000). Another sauropod tooth is a worn brachiosaurid tooth found in the Jinju Formation (Lim *et al*., 2001). Therefore, these remains indicate that at least four different sauropod taxa inhabited the region during the Gyeongsang Supergroup deposition. Although euhelopodid, barchiosaurid, and titanosaurid remains are present in the Gyeongsang Supergroup, these animals cannot be candidates for the Jageun Guhakpo trackmaker. The trackmaker more likely belonged to the Diplodocoidea or the Macronaria or the Camarasauromorpha of the Neosauropoda, judging from the synapomorphies of the trackway. Although a camarasaurid was reported based on a single worn tooth from the Gyeongsang Supergroup, it is not certain that a camarasaurid could be a candidate because camarasaurids are not known with certainty except in the Morrison Formation (Late Jurassic) of North America (Upchurch *et al*., 2004). Therefore, it is more reasonable that Jageun Guhakpo trackmaker was a member of the Diplodocidea or the Macronaria although the skeletal evidence for either group is not yet reported in the Gyeongsang Supergroup.

EVIDENCE OF "SWIMMING" SAUROPOD IN UHANGRI TRACKSITE

Recently Thulborn (2004) questioned the manus-only sauropod tracks in the Uhangri Formation (Upper Cretaceous), Korea described by Lee and Huh (2002). He gave a different opinion about the track identification and the origin of manus-only sauropod trackway than Lee and Huh's interpretation. First, he alleged that the tracks are not necessarily manus prints, but would equally well be interpreted as sauropod pes prints. He considered the great size of the Uhangri tracks (71 to 77.6 cm in diameter) and that the pes prints often appear circular in outline like manus prints. He therefore argued that the Uhangri tracks would be appropriate for pes prints rather than manus prints (Thulborn, 2004, p. 295). However, circular impressions are much more common in sauropod manus tracks than pes tracks (Ishigaki, 1989, fig. 9.2; Lee *et al*., 2000, fig. 6). The continuously sloping surface around the Uhangri circular footprint clearly indicates that the track was made by a round foot. It is unlikely that these rounded Uhangri tracks can be roughly oval-shaped sauropod pes prints in outline (narrower behind) with claw impressions strongly compressed transversely at the proximal end. Although sauropod pes prints could appear as subcircular basins without much detail in poorly preserved trackway or underprints, they are not in the case of the Uhangri tracks because they all are true prints, not underprints (Lee and Huh, 2002, p. 561). In addition, the Jageun Guhakpo sauropod tracks in this paper resolve the manus dimension and morphology of Uhangri tracks. The great diameter of manus prints of the Jageun Guhakpo trackway, 63 to 72 cm, roughly matches that of the Uhangri tracks. If the manus/pes ratios of Jageun Guhakpo tracks are applied to the Uhangri prints, pes prints of the Uhangri sauropod would be predicted to reach at least 1.2 m long at the site. No prints of such size or morphology have been found at the Uhangri site.

THE ORIGIN OF MANUS-ONLY SAUROPOD TRACKWAYS

Sauropod trackways dominated by manus impressions are quite common from the Middle Jurassic to the Late Cretaceous around the world (Bird, 1944, 1985; Ishigaki, 1989; Pittman, 1989; Lockley *et al*., 1992a; Lockley and Santos, 1993; Lockley *et al*., 1994b; Lockley *et al*., 1994c; Santos *et al*., 1994; Vila *et al*., 2005). These manus-dominanted trackways initially were interpreted as having been made by sauropod dinosaurs that floated their hindquarters while walking along the bottom with their forelimbs (Bird, 1944, 1985; Coombs, 1975; Ishigaki, 1989; Thulborn, 1990; Czerkas and Czerkas, 1990; Norman, 1991). This explanation was challenged by a 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. Vila *et al*. (2005) reported that a manus-only trackway (underprints) from the Upper Cretaceous Fumanya tracksite in Spain shows an identical arrangement of manus prints as a more complete trackway (manus-pes) from the same site. However, Uhangri tracks are clearly not underprints, but true manus prints of sauropods. 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. 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.

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 in the normal gait shown by the Jageun Guhakpo sauropod trackway. In addition, 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), suggesting quiet water conditions. The exclusive occurrence of these large footprints possibly implies that water was too deep for small animals to reach the bottom (Currie, 1983).

All evidence from the Uhangri tracks is suggestive of floating animals punting along a muddy bottom with their front feet. Extra buoyancy probably made large sauropod dinosaurs change the gait sequence and the timing of limb movement. Recently Henderson (2004) successfully demonstrated with computer modeling that floating *Brachiosaurus* and *Camarasaurus*, with their sub-horizontal trunks and their elevated hind feet, could have produced manus-only trackways. The sauropod ability to float could have helped them to survive when crossing shallow lakes or river beds intentionally, or escaping from predators.

EXPLANATION OF EXTRAMORPHOLOGICAL FEATURES OF UHANGRI SAUROPOD TRACKS

One hundred five sauropod manus prints in the Uhangri Formation exhibit an unusual pattern of morphology, with the interior of each print partitioned into a series of pockets by conspicuous radial crests. The floor of each print is raised into a starburst pattern of crests radiating from the center towards the outer margin, making an extraordinary morphology. Although these extramorphological characteristics were suggested to be radial crack features associated with underlayers where the foot indents slightly compact sandy layers in contact with an underlying muddy layer (Lockley *et al.*, 1989; Lockley, personal communication), it is clear as described above, that Uhangri tracks are not underprints. Lee and Huh (2002) argued that the complex system of crests and intervening pockets were made during 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.

However, a new interpretation on this unusual internal structure within the tracks was proposed by Thulborn (2004). He alleged that "fluid displacement and fracturing cannot be responded by a single physical force (impact of the trackmaker's foot) and it is difficult to envisage a substrate sufficiently plastic to be displaced into a raised rim encircling the footprint and, at the same time, sufficiently rigid as to respond by fracturing in a starburst pattern" (Thulborn, 2004, p. 296). However, all Uhangri tracks are large basin-like depressions, NOT surrounded by a raised rim (bourrelet) of displaced sediment (Lee and Huh, 2002, p. 559). There is no raised rim of displaced sediment at all in Uhangri tracks, and they are totally different from, for example, *Brontopodus birdi* from the Glen Rose Limestone (Farlow *et al.*, 1989) and Jageun Guhakpo sauropod tracks (Fig. 5). Thulborn's unwarranted assumption likely came from an incorrect interpretation of the illustrations of Lee and Huh's paper rather than direct observation from visiting the tracksite. Nevertheless, Thulborn (2004) proposed two alternative models of footprint formation. The first is the "milk skin" model (Fig. 6A). The superficial layer of the substrate was drawn up and stretched into a tent-like canopy (in much the way that the skin formed on heated milk will adhere to a fingertip) as the trackmaker's foot was lifted, and high enough, the adhering sheet of superficial layer collapsed into radiating folds in the interior of the footprint (Thulborn, 2004, p. 297). However, this model could not work successfully in the Uhangri tracks themselves. First of all, it does not seem that the trackmaker's foot is likely to have generated a strong lift as it was withdrawn from the elastic yet firm superficial layer. To make such a strong stretch possible, the sediment should be very adhesive and sticky. And deformation of the sediments detached off the trackmaker's foot forms usually an irregular area of relief as reported in Woodbine ornithopod tracks (Lee, 1997). Thulborn mentioned that a circular plateau at the focus of the radiating ridges (Lee and Huh, 2002, track number 12) is a scar mark torn away from the underside of the trackmaker's foot or a voided water vent created as the blister ruptured. But this feature is not observed in the other 104 tracks at all. It is more likely this could be a distorted feature of the crack center. The intervening pockets between crests have very smooth, gently sloping marginal walls which contain very fine vertical striations. These vertical striations indicate that the footprint was made by direct contact of trackmaker's sole with the substrate. In addition, it is very difficult to envisage that the elastic yet firm upper surface layer was stretched into a tent-like canopy under water, or even in the air, either.

Thulborn's second proposal is a "blister" model (Fig. 6B). It is not necessary to require the substrate to adhere to the trackmaker's foot. Instead, the impact and withdrawal of the foot drove water out of the footprint's floor and initiated a rapid backflow, resulting in a blister. The blister, then subsided gradually, allowing the distended canopy of sediment to collapse into a series of radial folds. The second model is essentially similar to the first model in terms of making a canopy of sediment. Again, it is very difficult to accept that the superficial layer of the substrate could be lifted up to make the distended dome only by a

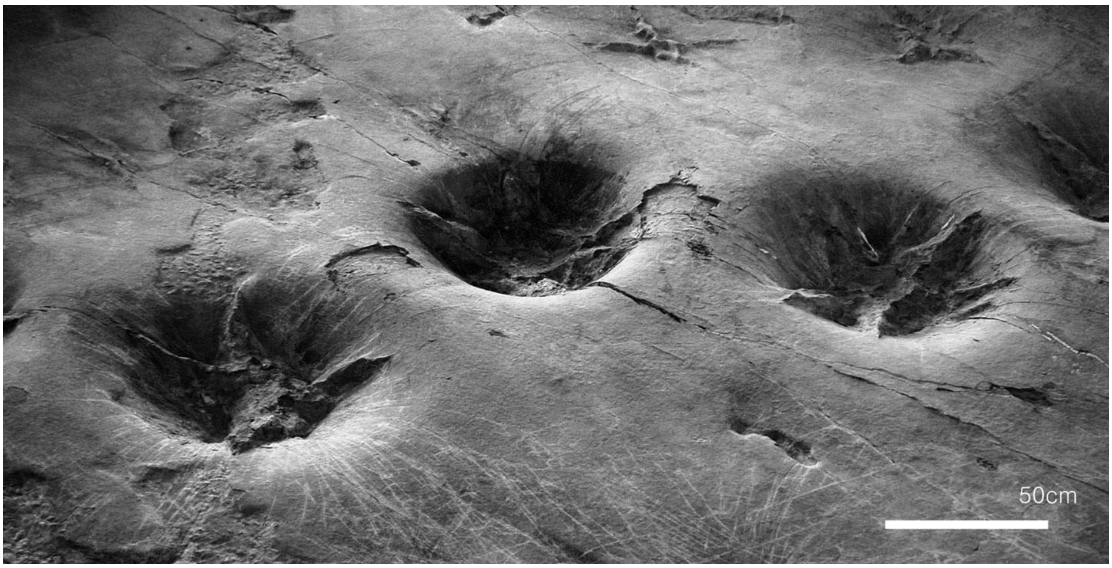

Fig. 5. Photographs of track number 9, 10, 12 from Uhangri manus-only sauropod tracks (see figure 5 in Lee and Huh, 2002).

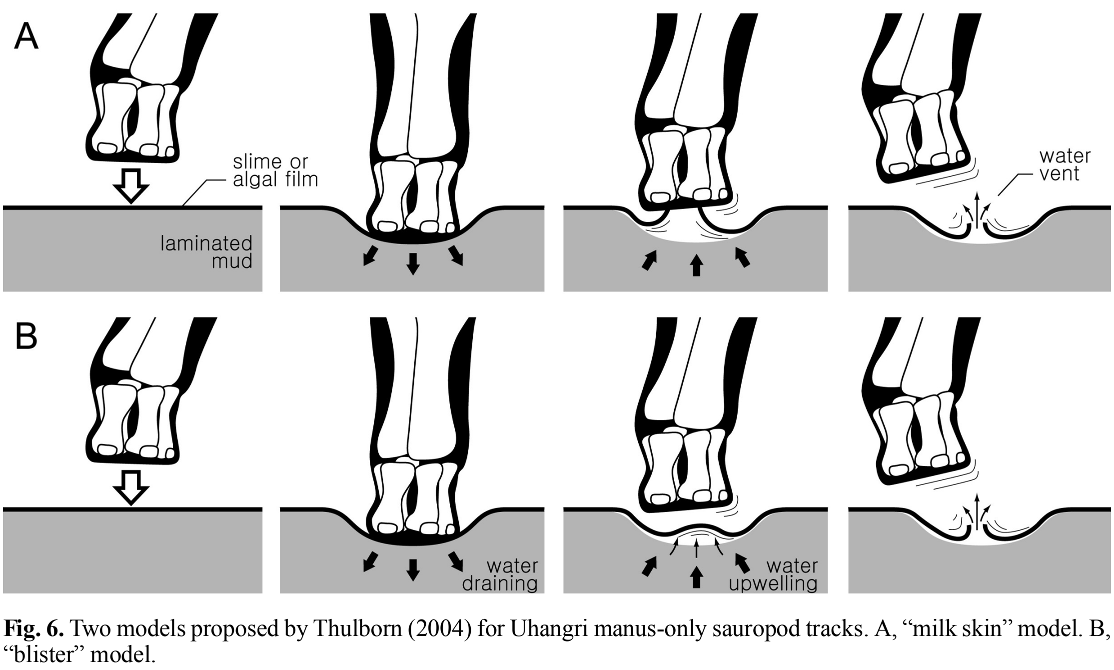

Fig. 6. Two models proposed by Thulborn (2004) for Uhangri manus-only sauropod tracks. A, "milk skin" model. B, "blister" model.

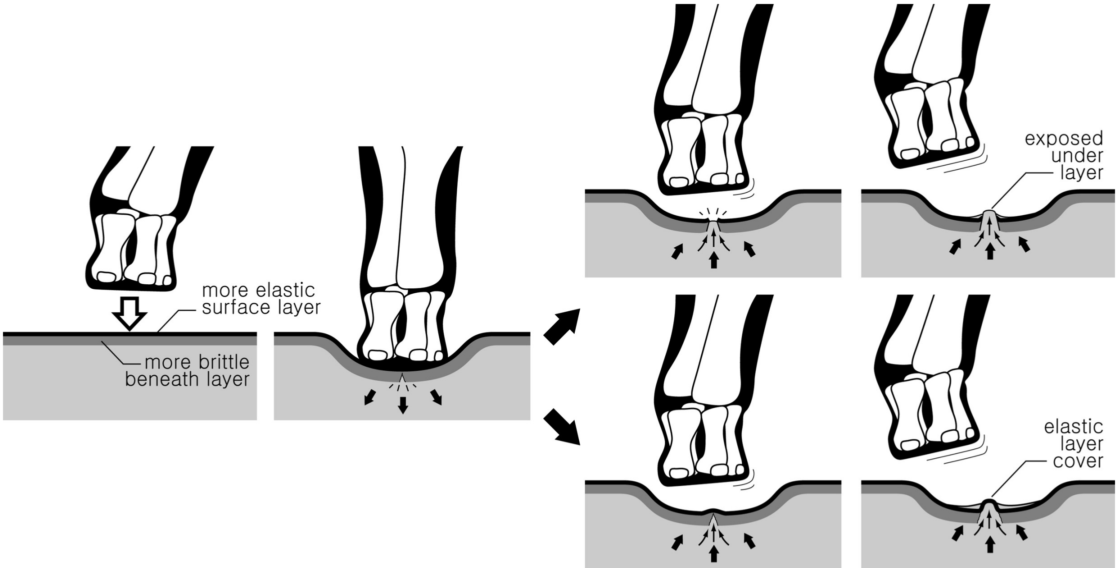

Fig. 7. The "cracked-open" model proposed originally by Lee and Huh (2002) for Uhangri manus-only sauropod tracks.

rapid water influx. To satisfy these two "canopy" models, the composition of crests should be the same as the surface layer. But, waterlogged mud beneath the surface layer is different from the surface layer lithologically. The lower layer is slightly coarser than the upper layer, and in fact, the crests consist of the coarser lower layer.

The model proposed by Lee and Huh (2002) is as follows (Fig. 7). The substrate on which the trackmaker walked was elastic yet firm to retain low tensile strength. The impact and downward force of the trackmaker's foot fissured the substrate layer to create cracks with a radial pattern. It is noticeable that the size of the crests in footprints is directly proportional to the depth of the tracks, indicating that the greater downward force produced the more prominent crests by wider crack opening. After the foot was lifted, waterlogged mud beneath the surface layer extruded up slowly through fissures on the floor of the footprint by dynamic stability. The bottom of the track may have bounced a little upward by this extrusion. This conclusion is reinforced by fine vertical striations left when the underlayer mud extruded through cracks, which are observed on the walls of crests (Fig. 8). In addition, the crests, even the extremities of crests, are not continuous with the undisturbed bedding plane but contact roughly along the crack lines. These extremities indicate that their surfaces were not completely opened but just lifted up by extrusion of underlayer mud. The inconsistency in arrangement and fine texture of crests clearly shows that these internal crests of the footprints were made by the extrusion of underlayer mud, not by collapsed radial folds. Therefore, extramorphological features of Uhangri sauropod manus tracks, starburst crests, are accumulation of extruded sediment through radial fissures (Fig. 9).

CONCLUSIONS

The Jageun Guhakpo sauropod tracks represent largest pes prints in Korea. A sauropod dinosaur belonging to the Diplodocidea or the Macronaria can be suggested as a candidate for the Jageun Guhakpo trackmaker based on skeletal and ichnological synapomorphies, animal size, and provenance. The Jageun Guhakpo sauropod tracks resolve the manus dimension and morphology of manus-only Uhangri sauro-

Fig. 8. A, an isolated manus-only trackway next to 105 manus-only sauropod tracks. B, an enlarged photograph of track number 1 of photo A to show the internal crests. C, vertical striation shown in the wall of crest of track number 1. D, an enlarged photography of track number 2 of photo A to show internal crests. E, vertical striation shown in the wall of crest of track number 2.

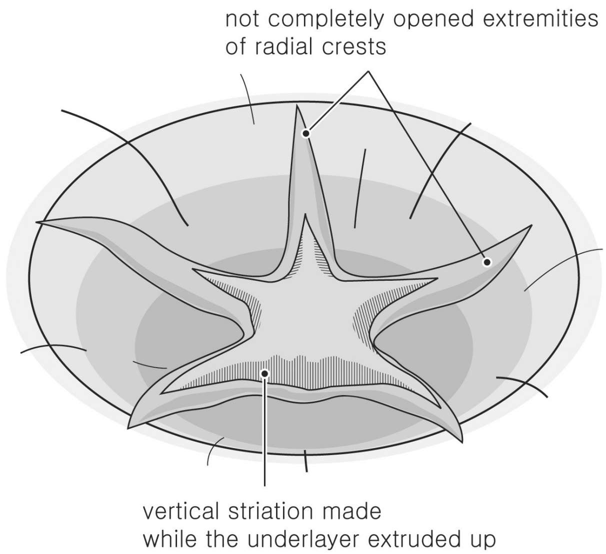

Fig. 9. An illustration to show detailed extramorphological features of a typical Uhangri manus-only sauropod track.

pod tracks. The floor of each Uhangri print is raised into a starburst pattern of crests radiating from the center towards the outer margin, making an extraordinary morphology. These features can be much more reasonably explained by “cracked-open” model rather than “canopy” model recently proposed.

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경상남도 고성군 동해면에서 산출된 용각류 보행렬과 우항리의 용각류 앞발자국에 대하여 그 것이 가지는 고생물학적 의미

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요 약: 작은 구학포의 용각류 발자국 보행렬은 8 m에 걸쳐 11개의 연속적인 발자국으로 구성되어 있다. 평균 앞발자국의 길이와 폭은 각각 64.4 cm, 67.0 cm 이다. 앞발자국은 첫 번째 발가락 끝에 발톱자국이 없는 둥근 형태다. 다섯 번째 발가락은 첫 번째 것보다 약간 더 크며 두 번째 발가락에서 네 번째까지 발가락은 분리된 형태를 보이지 않는다. 평균 뒷발자국의 길이와 폭은 각각 112.3 cm와 95 cm 이며 한국에서 가장 큰 공룡 뒷발자국이다. 안쪽 보행렬 폭은 분명하게 “narrow gauge” 패턴을 보인다. 골격과 발자국의 진화된 특징, 몸의 크기, 서식지에 기초해 판단할 때 작은 구학포의 용각류 발자국을 남긴 용각류는 Diplodocidea 혹은 Macronaria에 속하는 것으로 추정된다. 작은 구학포의 용각류 발자국은 우항리 용각류 발자국이 몸의 뒷부분은 뜬 채 앞발을 이용해 물속에서 걸은 진짜 앞발자국임을

지시한다. 우항리의 발자국 안에는 중심에서 외부로 별 모양으로 뻗어나가는 가지를 가진 독특한 형태를 가진다. 이러한 방사선의 가지와 그 사이의 공간이 만드는 복잡한 구조는 공룡이 발을 밟았을 때 다소 단단한 지표가 깨지고 그 깨진 사이로 아래의 덜 고화된 진흙이 솟아올라 만들어진 것이다. 가지가 지표의 것보다 더 조립질이며 가지의 옆면에는 관찰되는 미세한 수직 선구조들은 이러한 해석에 중요한 증거들이다. 그러므로 우항리 용각류발자국의 독특한 내부구조는 최근에 제안된 "천개(天蓋)" 이론보다는 "열개(裂開)" 이론에 의해 더 합리적으로 해석된다.

주요어: 용각류발자국, 작은 구학포, 고성, 우항리, 수영

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