제주도의 신생대 하모리층에서 발견된 포유류와 조류 발자국 화석 및 무척추동물의 생흔화석에 관한 고생물학적 연구

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〈 목 차 〉

〈 연구계획 요약문 〉

중심어	포유류 발자국 화석	조류 발자국 화석
	생혼 화석	후기 신생대
	제주도	하모리층

연구목표	1. 하모리층에서 산출되는 포유류와 조류 발자국 화석 및 무척추동물의 생혼화석에 대한 산출 상태 조사 및 기재 2. 발자국 화석 연구를 통한 척추동물의 다양성과 고생물군집 규명 3. 척추동물의 발자국 화석과 무척추동물의 생혼화석 및 퇴적상 분석에 의한 고환경과 고생태의 복원

연구내용	본 연구는 크게 3개의 내용으로 구성된다. 1) 제주도의 후기 신생대 (제4기) 하모리층에서 우제류(사슴류)와 기제류(말) 등의 발자국 화석 수 천여 점과 다양한 새 발자국 화석이 백여 점 이상 발견되었으며, 세계적으로 산출이 드물며 신생대 지층에서는 세계 최초로 보고되는 물고기에 의한 생혼화석과 절지 동물의 보행열 등의 무척추동물의 생혼화석이 다양하게 산출된다. 특히 현재까지 우리 나라에서는 포유류 발자국 화석에 대한 보고나 연구는 전혀 없었으며, 세계적으로도 포유류 발자국 화석은 중생대 공룡 발자국 화석에 비해 주목받지 못한 체로 남아 있다. 따라서 기존의 국내·외 연구 자료를 검토하고, 본 지역에서 나타나는 발자국 화석에 대한 자세한 산출 상태를 조사하고 체계적인 분류와 기재를 실시하고자 한다. 2) 현재 살아있는 척추동물의 발자국에 대한 연구 결과, 생존하고 있는 대부분의 동물들은 일반적으로 개체수가 많은 동물이 그에 비례하여 발자국을 많이 남기며, 동물의 다양성은 발자국의 다양성으로 나타난다는 것이 밝혀졌다. 따라서 발자국 화석에 대한 연구를 통해 당시의 개체수와 다양성 및 고생물군집을 간접적으로 규명하고자 한다. 3) 화산 활동으로 형성된 제주도의 해안가에서 포유류, 조류 그리고 무척추동물 등 다양한 생물들이 왜, 어떻게 공존하며 살았는지를 그들의 발자국에 나타난 행동 양식과 무척추동물의 생혼화석 및 퇴적상 분석을 통해 고환경과 고생태를 규명하고자 한다.

기대효과 (응용분야 및 활용범위 포함)	1) 우리 나라에서 최초로 수행되는 포유류의 발자국 화석에 관한 기재와 분류는 중국, 한반도, 일본을 연결하는 동북 아시아 지역 및 동남 아시아 지역에서 산출되는 포유류 발자국 화석의 비교 연구에 매우 중요한 자료로 활용될 것으로 생각된다. 2) 포유류는 비교적 넓은 지역에 걸쳐 서식하므로 제주도의 발자국 화석은 한반도, 중국, 일본 등의 신생대 지층 대비에 유용하게 활용될 것이다. 3) 우제류(사슴, 노루 등)와 기제류(말)의 발자국 화석은 제주도에서 자생하는 사슴과 노류 및 제주 조랑말의 기원과 고생태 복원에 대한 중요한 단서를 제공할 것으로 생각된다. 4) 본 연구의 결과는 학생들을 위한 현장 교육 실습장으로서, 그리고 제주도를 방문하는 국내·외의 일반인들을 위한 관광 자원으로 활용될 것을 기대한다.

〈 연구결과 요약문 〉

중심어	포유류 발자국 화석	조류 발자국 화석
	생흔 화석	후기 신생대
	제주도	하모리층
연구목표	1. 하모리층에서 산출되는 포유류와 조류 발자국 화석 및 무척추동물의 생흔화석에 대한 산출 상태 조사 및 기재 2. 발자국 화석 연구를 통한 척추동물의 다양성과 고생물군집 규명 3. 척추동물의 발자국 화석과 무척추동물의 생흔화석 및 퇴적상 분석에 의한 고환경과 고생태의 복원	
연구내용	본 연구는 크게 3개의 내용으로 수행되었다. 1) 제주도의 하모리층에서 조류와 우제류(사슴류)의 발자국 화석에 대한 산출 상태를 조사하고, 체계적으로 분류하고 기재하였다. 본 연구 지역에서 산출되는 척추동물의 발자국은 기재된 조류와 우제류 발자국 이외에도 사람 발자국, 장비류로 추정되는 발자국, 육식동물로 추정되는 발자국 등이 발견되었다. 2) 척추동물의 발자국과 무척추동물의 생흔화석 그리고 실체화석에 대한 개체수 분석 등을 통하여, 과거 제주도 하모리층이 생성될 당시의 생물의 개체수와 다양성 및 고생물군집을 규명하였다. 3) 화산 활동으로 형성된 제주도의 해안가에서 포유류, 조류 그리고 무척추동물 등 다양한 생물들이 왜, 어떻게 공존하며 살았는지를 척추동물 발자국, 무척추동물의 생흔화석 그리고 실체 화석 및 퇴적구조의 분석을 통해 고환경과 고생태를 규명하였다.	
연구성과	1) 제주도의 하모리층에서 2속의 신속과 4종의 신종을 포함하여 8속 8종의 새 발자국, 1속 1종의 우제류 발자국, 1속 1종의 물고기 생흔 그리고 13속 16종의 무척추동물 생흔화석을 기재하였다. 2) 퇴적구조, 척추동물의 발자국 그리고 무척추동물의 생흔화석에 대한 분석을 통하여, 화석 산지의 하모리층은 얕은 해안가, 특히 반폐쇄된 석호 또는 조간대 환경에서 퇴적된 것으로 추측된다. 3) 생흔화석의 개체수 분석을 통해 하모리층에서 척추동물의 발자국은 우제류 발자국이 가장 풍부하고, 조류, 사람, 장비류(?), 그리고 육식동물(?)의 발자국 순서로 풍부하게 나타난다. 4) 복족류, 이매패류, 게 그리고 식물 화석 등의 실체 화석과 함께 척추동물 발자국과 무척추동물의 생흔화석을 분석한 결과, 하모리 생물군의 고생물군집과 고생태를 복원하였다.	

〈 EXECUTIVE SUMMARY 〉

Keywords	Mammalian footprints	Avian footprints
	Trace fossils	Late Cenozoic
	Jeju Island	Hamori Formation

Purpose	The main objectivies of this study is to (1) survey the distribution and occurrence of mammalian and avian footprints and invertebrate trace fossils from the Hamori Formation and to describe them systematically (2) recognize the diversity and paleocommunity of vertebrate and invertebrate animals by analyzing vertebrate footprints and invertebrate trace fossils (3) reconstruct the paleoenvironment and paleoecology by analyzing vertebrate footprints, invertebrate trace fossils and sedimentary faicies.
Contents	This study is composed of three contents as follows; 1) The occurrence and distribution of the avian, artiodactyla footprints and invertebrate trace fossils in the Hamori Formation of Jeju Island were surveyed and these trace fossils were systematically classified and described. In the study area, the vertebrate footprints such as hominid, proboscidean(?) and carnivore(?) footprints and unidentified footprints were discovered except for avian and artiodactyla footprints. 2) The abundance and diversity of fossil animals, and the paleocommunity of the Hamori Formation were recognized by analyzing the vertebrate footprints, invertebrate trace fossils and body fossils. 3) The paleoenvironment and paleoecology of the Hamori Formation were reconstructed by analyzing the sedimentary structure, vertebrate footprints and invertebrate trace fossils.
Expected Contribution	1) Eight ichnogenera and ichnospecies of avian footprints including two new ichnogenera and four new ichnospecies, one ichnogenus and ichnospecies of artiodactyla footprints, one ichnospecies of fish trail, and thirteen ichnogenera and sixteen ichnospecies of invertebrate trace fossils were systematically described from the Hamori Formation, Jeju Island. 2) The Hamori Formation of the fossil locality seems to be deposited in the shallow shore line environment, especially semi-closed lagoon or intertidal setting. 3) By examination of footprints abundance, deer-like artiodactyla footprints are most common and footprints attributed to birds, hominids, proboscidean(?) and carnivore(?) are less common in the Hamori Formation. 4) By analyzing diversity and abundance of vertebrate footprints and invertebrate trace fossils associated with body fossils including gastropods, bivalves, crabs and plants, the paleocommunity and paleoecology of the Hamori fauna were reconstructed.

〈 연구내용 및 결과 〉

INTRODUCTION

A renaissance of the study of fossil footprints has been driven by multitude of discoveries and the realization that vertebrate ichnology makes important contributions to our understanding terrestrial vertebrates (Lockley, 1991; 1998). The study of dinosaur footprints has undergone a remarkable renaissance in the last few decades. Dinosaur tracks are useful for interpretation of dinosaur behavior ranging from locomotion and speed (Alexander, 1976) to individual and social behavior (Lockley, 1995) and paleoecology (Lockley et al., 1992), paleoenvironments (Lockley, 1986), biostratigraphy (Lockley, 1998; Lockley et al., 1999; Olsen et al., 2002), and even dinosaur age (Matsukawa et al., 1999).

However, the mammalian and avian footprints of the Cenozoic Era, have not received much attention and relatively poorly understood compared with Late Paleozoic and Mesozoic reptilian tracks (Doyle et al., 2000). Paucity of reliable information of Cenozoic vertebrate tracks except that of living vertebrate tracks (e.g. Murie, 1974; Triggs, 1996) has probably been not due to paucity of tracks but due to much less attention has been devoted to tracks compared to vertebrate skeletons by vertebrate paleontologists. This may be supported by the thing that the Cenozoic Era is commonly known as the Age of Mammals or the Age of Birds.

Diverse and abundant mammalian footprints including the hominid, artiodactyla, proboscidean?, and carnivore? footprints, and unidentified vertebrate footprints type I and type II, over two hundreds avian footprints, fish trails, and numerous invertebrate trace fossils associated with fossil crabs, gastropods, bivalves and plants discovered for the first time from the shoreline deposits of the Hamori Formation of Jeju Island, Korea are herein reported. Of these trace fossils, the artiodactyla and the avian footprints and invertebrate trace fossils are the main subject of this study and named and systematically described as ichnotaxa using classification scheme. The main objectives of this study is to : (1) survey the distribution and occurrence of mammalian and avian footprints and invertebrate trace fossils from the Hamori Formation and to describe them systematically; (2) recognize the diversity and paleocommunity of vertebrate and invertebrate animals by analyzing vertebrate footprints and invertebrate trace fossils; (3) reconstruct the paleoenvironment and paleoecology by analyzing vertebrate footprints, invertebrate trace fossils and sedimentary faicies.

GEOLOGICAL SETTING

Jeju Island is a major Quaternary volcanic field in Korea. The island, 73 km long and 31 km wide, is mainly composed of plateau- and shield-forming lavas and is covered with numerous monogenetic volcanic cones (Park et al., 2000c; Fig. 1). Major sedimentary formations on the island, e.g. the Sinyangri Formation (Han et al., 1987) and the Hamori Formation (Park et al., 2000a), are also composed of mainly reworked hydrovolcanic materials and found near the hydrovolcanic centers. This implies that the hydrovolcanic centers were the major sources of clastic sediments and played an important role in generating the Quaternary depositional records on the island.

The Songaksan tuff (ST) and the Hamori Formation, which are the youngest units on Jeju Island, occur in the southwestern margin of the island above an extensive and low-altitude, plateau-forming basalt lava (Fig. 1). The ST rings/cones and the lava dome overlies by the Kwanghaeak Basalt (KB), which is characterized by abundant olivine phenocrysts and acicular feldspar laths and is tholeiitic andesite in composition (Park et al., 2000a). The geologic age of the KB has been known to be 0.6 Ma (Lee et al., 1988).

The Hamori Formation (Quaternary) is exposed along the northeast and west coasts of the Mt. Songak (Park et al., 2000a; Fig. 1). The Hamori Formation which was previously called the reworked tuff (Chough and Sohn, 1990) or volcaniclastic sediments (Kim et al., 1989) overlies the KB. According to Park et al.(2000b), the Hamori Formation gradually changed into the ST or unconformably overlies ST. However, the unconformable contact is not observed in the field. This may be supported by a recent report that there is no significant erosive event but continuous volcanic eruption in the Mt. Songak area (Won and Hwang, 2002).

On the basis of author's observation in the field and previous reports that the formation underlies and overlies the ST from place to place (e.g. Chough and Sohn, 1990), it is thought that

the Hamori Formation intergradationally changed into the ST. Consequently, the geologic age of the Hamori Formation can be estimated to be nearly same as that of the ST which was recently known to be 50,000 yr (Won and Hwang, 2002). This is, however, significantly different from the recent record on the age (about 4,000 yr) of the molluscs collected from the Hamori Formation in the west coast of the Mt. Songak (Sohn, 2002). This problem in the geologic age difference remains to be solved in the future.

The sedimentary facies of the Hamori Formation distributed in the west part of the Mt. Songak was recently analysed for interpretation of depositional environment (Sohn et al., 2002). According to them, the formation was deposited in a high-energy nearshore environment above a fair-weather wave base during and after the eruption of the ST (Sohn et al., 2002). However, the Hamori Formation of the northeast coast of the Mt. Songak is mainly composed of basaltic granule conglomerate, basaltic pebbly sandstone, tuffaceous sandstone and mudstone. Diverse sedimentary structures including wave ripple marks, adhesion ripple marks, Runzelmarken, desiccation cracks, planar stratification, and cross-stratification associated with footprints of humans, mammals, and aves, and invertebrate trace fossils observed in the measured section indicate low-energy shoreline environment.

The measured section of the Hamori Formation exposed in the northeast coast of the Mt. Songak shows the stratigraphic distribution of the lithology, sedimentary structures, footprints of the humans, mammals, and aves, and invertebrate trace fossils (Fig. 2)
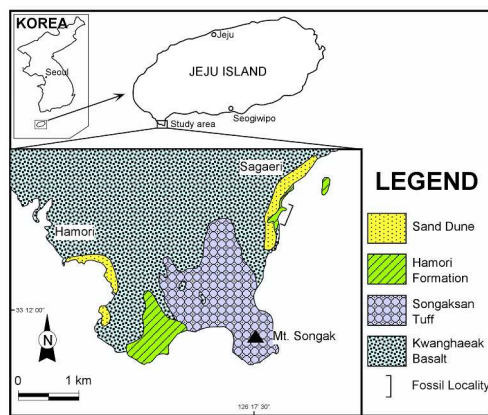

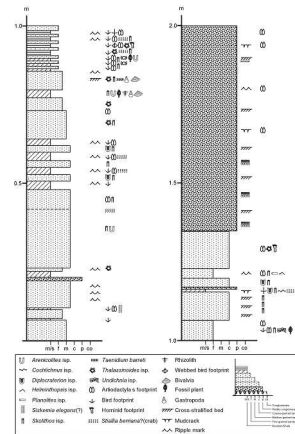Fig. 1. Geologic map showing distribution of the Hamori Formation and fossil locality (Park et al., 2002b).

Fig. 2. Measured section of the fossil locality.

SYSTEMATIC ICHNOLOGY
Mammalian Footprints
Bifidis jejuensis ichnosp. nov.
Fig. 3-a, b

Holotype : HDT_I-1 (Fig. 3-a), Hamori Formation, Jeju Island, Korea

Deriviation of name : After Jeju Island, location of footprints discovery, with reference to the *Bifidis* from Jeju Island, Korea.

Diagnosis : *Bifidis* with circular shape, prominent open v-shaped interdigital space between tapering, sharp pointed hooves and indistinct shallow proximal gap.

Description : Didactyl artiodactyl footprints of medium size, without pad impressions. Manus and pes are very similar in size and form. Impressions of two hooves shown mirror images form circular shape. Open v-shaped interdigital space is prominent. Digits tapered to sharp termination. Of the over one thousand of tracks, three well preserved trackways observed are measured. Lengths of tracks are 71 to 84 mm and widths are 58 to 84 mm. Pace, stride, pace angulation, and pace width are approximately 440 mm, 830 mm, 140°, and 140 mm respectively.

Remarks : *Bifidis jejuensis* compares in size with *Bifidis velox* Demathieu, Ginsburg, Guérin, and Truc, 1984, described from the Oligocene deposits of south eastern France (Demathieu et al., 1984). However, the present species is distinguished from *B. velox* in its circular shape, much open v-shaped interdigital space, position of maximum width in the middle of length, and shallowly

embayed proximal gap. On the basis of gait parameters including stride, it may be thought that deers, with trunk length about 80 cm, are likely to have produced the *Bifidis jejuensis.*

Fig. 3. Artiodactyla footprints from the Hamori Formation. a, b : Trackways of *Bifidis jejuensis* ichnosp. nov., ; c-j : Various type of artiodactyla footprints. Scale bars are 23mm in figure c-j.

Avian Footprints
Ardeipeda ichnosp.
Fig. 4-a

Figured specimen : HBT-002-1

Description : *Ardeipeda* tracks of intermediate to large size exhibiting straight central digit (Ⅲ) and two straight lateral digits (Ⅱ and Ⅳ). Central digit is equal to subequal in length to lateral digits, 30 to 55 mm in length. Digit Ⅰ is prominent and short, 8 to 19 mm in length. Axis of digit Ⅰ almost corresponds with that of digit Ⅲ. Interdigital angles between digit Ⅱ and Ⅳ are 125° to 130°. All digits are united proximally. Imprints of web are not observed. Pes length and width are 28 to 75 mm and 31 to 78 mm respectively.

Remarks : This track compares in overall shape and size with *Ardeipeda egretta* Panin and Avram, 1962, but it differs from this in its nearly equal in the lengths of lateral digits (Ⅱ and Ⅳ) and central digit (Ⅲ).

Avipeda ichnosp.
Fig. 4-b

Figured specimen : HBT-001-1-2

Description : *Avipeda* tracks comprising impressions of a straight central digit (Ⅲ) and straight to slightly curved lateral digits (Ⅱ and Ⅳ). Pes lengths are 61 to 65 mm and widths are 60 to 67 mm. Central digit (Ⅲ) is longest, 54 to 60 mm in average length. Lateral digits (Ⅱ and Ⅳ) are nearly equal in length, 41 to 48 mm in average. Interdigital angles between digits Ⅱ and Ⅳ are much narrow, 70 to 73 degrees. Phalangal pads of digits and hill pads are observed. Impression of hallux and interdigital webbing are not observed.

Remarks : These footprints do not compare well to currently known species of *Avipeda*, *A. adunca* Sarjeant and Langston, 1994, *A. ipolyensis* (Kordos, 1983), and *A. phoenix* Vialov, 1965.

These tracks are different from *Avipeda adunca* described from the Late Eocene of Texas (Sarjeant and Langston, 1994) in their much more acute interdigital angle (about 72°) and much larger footprint size. The footprints also differ from *Avipeda phoenix* from the Miocene of Ukraine (Vialov, 1965) in their very much more acute interdigital angle and very much larger footprint size. Length and width of tracks and interdigital angle of avian footprints described as *Avipeda* ichnosp. A and *A.* ichnosp. B from the Late Miocene Cooper Caynon Formation (Scrivner and Bottjer, 1986) compare with those of the Hamori avian tracks, though their interdigital angles are not clearly documented. These footprints, however, differ in overall shape and size to specimens described as *Avipeda* ichnosp. C, *A.* ichnosp. D., and *A.* ichnosp. E (Scrivner and Bottjer, 1986).

Gruipeda koreanensis ichnosp. nov.
Fig. 4-c

Holotype : HBT $_\mathrm{I}$-L$_1$, brownish shale bed of the Hamori Formation, Jeju Island.

Paratype : HBT $_\mathrm{I}$-R$_2$, same as Holotype.

Deriviation of name : After Jeju Island, site of the footprints discovery, with reference to the *Gruipeda* from Jeju Island, Korea.

Diagnosis : Avian footprints of very large size exhibiting four digits, three of which (Ⅱ to Ⅳ) are directed forward and large, the fourth (Ⅰ) directed backward, relatively long. The interdigital angles between digits Ⅱ and Ⅳ are 110 to 123°. The axis of digit Ⅰ corresponds with that of digit Ⅲ. Impressions of webbing absent. All digit (Ⅰ-Ⅳ) are commonly united proximally.

Description : Relatively large *Gruipeda* tracks comprising impressions of three nearly straight forward digits (Ⅱ- Ⅳ) and a relatively long backward digit (Ⅰ). Pes lengths are up to 150 mm
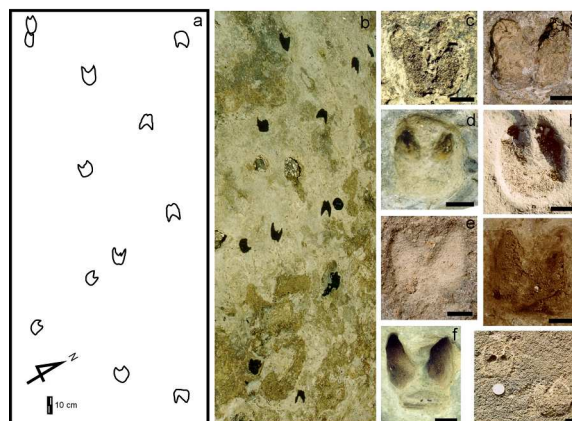
and widths are 122 mm in average. Central anterior digit (Ⅲ) is longest, 72 mm in average length. Lateral digits (Ⅱ and Ⅳ) are different in size, 47 mm and 56 mm in average respectively. Prominent backward digit Ⅰ is 40 mm in average. Interdigital angles between digits Ⅱ and Ⅳ are 117° in average. Posterior digit (Ⅰ) is well preserved and directed backward the mid-line of track. All digits (Ⅰ-Ⅳ) are commonly united proximally. Impressions of webbing are not observed.

One well preserved trackway observed is about 1,200 mm long and comprises six individual footprints. Pace, stride, pace angulation, and pace width of trackway are 211 mm, 333 mm, 79°, and 152 mm in average respectively.

Remarks : Panin and Avram (1962) erected *Gruipeda maxima* from the Miocene deposits of Ciscarpathian Mtns., Rumania. *Gruipeda intermedia* was erected from the Miocene of Rumania (Panin, 1965). Sarjeant and Langston (1994) regarded that *Urmiornis abeli* Lambrecht, 1938, from the Pliocene of Iran, *Chardriipeda becassi* Panin and Avram, 1962, *C. disjuncta* Panin and Avram, 1962, *C. minima* Panin and Avram, 1962, *C. minor* Panin, 1965, and *Avipeda filiportatis* Vialov, 1965, should be changed into *Gruipeda abeli, G. becassi, G. disjunta, G. minima, G. minor,* and *G. filiportatis* respectively. Sarjeant and Langston (1994) also erected a new ichnospecies of *Gruipeda, G. calcarifera,* from the Late Miocene of Trans-Pecos Texas.

Of these several species of *Gruipeda*, present footprints nearly close to *G. maxima* in the point of size of tracks, interdigital angles between digits Ⅱ and Ⅳ. However, *G. koreanensis* is very different from *G. maxima* in its much longer digit Ⅰ, equal in interdigital angles between digits Ⅰ and Ⅱ and between digits Ⅰ and Ⅳ, and all of digits (Ⅰ-Ⅳ) united proximally. These morphological character which cannot compare to any currently known species of *Gruipeda* allows the Hamori footprints to be assigned as to *G. koreanensis* ichnosp. nov. herein described.

Ignotornis ichnosp.
Fig. 4-d

Figured specimen : HBT-003-01

Description : Avian tracks comprising impressions of a central digit (Ⅲ), two lateral digits (Ⅱ and Ⅳ), and a hallux (digit Ⅰ). Pes length is 27 mm and width is 24 mm. Central digit (Ⅲ) is longest, 15 mm. Length of digit Ⅱ is 12 mm, slightly longer than that of digit Ⅳ, 9 mm. Interdigital angle between digits Ⅱ and Ⅲ (about 60°) is wider than that between digits Ⅲ and Ⅳ (about 50°). Digit Ⅰ is relatively short. Interdigital angle between digits Ⅰ and Ⅱ (about 100°) is markedly narrower than that between digits Ⅰ and Ⅳ (about 140°). Axis of digit Ⅰ nearly corresponds to that of digit Ⅲ. Impression of web is restricted to the proximal part of the interdigital angles.

Remarks : This track quite resembles *Ignotornis mcconnelli* Mehl, 1931, described from the Dakota sandstone of Colorado (Mehl, 1931) in general outline, but it differs from this in its much smaller size, absence of prominent claw impression, and wider interdigital angles between digits Ⅱ and Ⅳ. This track is also different from bird track designated as *Forma* E from the Oligocene deposits of Spain (Casanovas-Caldellas and Santaffe-Llopis, 1982) in its prominent hallux impression.

Koreanornipodichnus ichnogen. nov.

Type species : *Koreanornipodichnus cheongi*

Derivation of name : Korea, country of footprints discovery, Latin, orni for ave, and Latin, ichnus for tracks ; with reference to bird tracks of Korea.

Diagnosis : Avian footprints of moderate to large size and anchor-like shape comprising a straight and thick central digit (Ⅲ) and two smoothly curved and thick lateral digits (Ⅱ and Ⅳ). Length of digit Ⅲ is nearly same as that of digits Ⅱ and Ⅳ. Thickness of each digit is nearly consistant except termination with claw impression. Impressions of forward digits Ⅱ to Ⅳ are prominently united at the base of footprints. Interdigital angles between digits Ⅱ and Ⅳ are up to 140°. Impressions of digit Ⅰ uncommonly observed are relatively short and separated. The axis of digit Ⅰ corresponds to that of digit Ⅲ. Webbing is partially developed only at the proximal part.

Remarks : *Koreanornipodichnus* superficially compares in overall shape and size to some of bird tracks reported from the Eocene Green River Formation of Utha (Moussa, 1968, Plate 177, Fig.1). Bird footprints from the Pliocene Motoaikai Formation of Japan (Yoshida, 1967) resemble *Koreanornipodichnus* in their general outline, but they differ from this in their larger size. Interdigital angles between digits Ⅱ and Ⅳ of Japanese bird footprints (Yoshida, 1967, Plate Ⅱ, Fig.

1-2) are nearly comparable with those of *Koreanornipodichnus*, though Yoshida (1967) mentioned the interdigital angles between digits II and III and between digits III and IV are about 90°. Yoshida (1967) regarded that Motoaikai footprints may have been impressed by white-naped Crane or some allied species, when they were feeding and trotting along the shoreline or on the ripple-marked shallow bottom.

Koreanornipodichnus markedly differs from bird tracks from the Paleocene Fort Union Formation of Wyoming (Johnson, 1986, Type 1 of Fig. 2-B) and bird tracks from the Oligocene deposits of Spain (Casanovas-Caldellas and Santaffe-Llopis, 1982, *Forma* D in Fig. 3) in its much reduced web impression and axis of hallux impression corresponding that of central digit.

Koreanornipodichnus   cheongi ichnosp. nov.
Fig. 4-e

Holotype : HBT$_I$-R$_1$, Hamori Formation, Jeju Island, Korea.

Paratype : HBT$_I$-L$_1$, same as Holotype.

Deriviation of name : After the Korean paleontologist and stratigrapher Cheong, C. H. (1920-), whose kind guidance enabled the author to study the Hamori footprints.

Diagnosis : same as diagnosis of ichnogenus, *Koreanornipodichnus.*

Description : Avian tracks comprise a straight central digit, two slightly curved lateral digits, and a hallux impressions. Length of pes is 49 to 55 mm and width is 80 to 81 mm. Central digit is 45 to 48 mm long and lengths of lateral digits II and IV are 34 to 37 mm. Thickness of digits is up to 5 mm. Claw impressions are observed at the end of digits. Impressions of digits II to IV are distinctively united at the proximal part and they look like an anchor. Interdigital angles between digits II and IV are about 140°. Impressions of digit I are uncommonly observed and they are shorter than those of central digit. The axis of digit I nearly corresponds to that of digit III. Webbing impressions are partially observed only at the proximal part.

Remarks : As mentioned previously, so far as the authors know, none of bird tracks currently known compares well with *Koreanornipodichnus cheongi* in morphology.

Ornipodichnus ichnogen. nov.

Type species : *Ornipodichnus hamoriensis*, Late Pleistocene Hamori Formation, Jeju Island, Korea

Deriviation of name : Latin Orni for ave, Latin pod for foot, and Latin ichnus for track; with reference to the avian footprints.

Diagnosis : Avian tracks of moderate size, exhibiting three forward digits. Central digit (III) is longest. Interdigital angles between digits II and IV are about 115°. Impressions of digit I are not observed. Three forward digits (II-IV) are distinctively separate. Webbing absent.

Remarks : *Ornipodichnus* is clearly distinguished from the avian footprints with web, such as *Anatipeda* Panin and Avram, 1962, *Charadriipeda* Panin and Avram, 1962, *Roepichnus* Doyle, Wood, and George, 2000, *Hwangsanipes* Yang, Lockley, Greben, Erickson, and Lim, 1995, and *Uhangrichnus* Yang, Lockley, Greben, Erickson, and Lim, 1995. In the absence of distinct hallux impressions, *Orinipodichnus* may be distinct from *Gruipeda* Panin and Avram, 1962, *Antarctichnus* Covacevich and Lamperein, 1970, *Ardeipeda* Panin and Avram, 1962.

Ornipodichnus differs from *Avipeda* Vialov, 1965, in its much wider interdigital angles between digits II and IV. *Pulchravipes* Demathieu, Ginsburg, Guérin, and Truc, 1984, compares with *Ornipodichnus* in general outline and size, but the former is markedly different from the latter in its much wider interdigital angles between digits II and IV (ranging from 125° to 145°). *Ornipodichnus* is also different from *Fuscinapeda* Sarjeant and Langston, 1994 in its absence of prominent hill impression and united digits, and from *Iranipeda* Vialov, 1989 in lack of distinct hill pad impression and consistently diverging tracks.

Ornipodichnus hamoriensis ichnosp. nov.
Fig. 4-f

Holotype : HBT$_V$-R$_1$, Hamori Formation, Jeju Island, Korea

Paratype : HBT$_V$-L$_2$, same as holotype.

Deriviation of name : After Hamori, location of the footprints discovery, with reference to the *Ornipodichnus* from the Hamori, Jeju Island, Korea.

Diagnosis : Avian footprints of moderate size, showing three straight digits (II to IV) with

moderate thickness and pointed termination. Central digit (Ⅲ) is longest, about 25% longer than the nearly equal sized lateral digits (Ⅱ and Ⅳ). Interdigital angles between digits Ⅱ and Ⅳ are about 115° in average. All digits are distinctively separated. Hallux impressions are not observed. Webbing absent.

Description : Of the numerous specimens observed in the field, five distinct trackways of *Ornipodichnus hamoriensis* are recognized. Trackways designated as HBT_Ⅴ to HBT_Ⅸ comprise 6, 4, 4, 3, and 6 individual footprint respectively. HBT$_{Ⅱ-Ⅲ, Ⅴ-Ⅶ}$. Pes length, pes width, length of digits Ⅱ, Ⅲ, and Ⅳ, and interdigital angles between digits Ⅱ and Ⅳ are 24-30 mm, 31-40 mm, 16-20 mm, 20-26 mm, 16-20 mm, and 108-120° respectively. Pace, stride, pace angulation, and pace width of *Ornipodichnus hamoriensis* are markedly variable in each trackway (HBT$_{Ⅱ-Ⅲ, Ⅴ-Ⅶ}$).

Remarks : Some of footprints described as *Pulchravipes magnificus* Demathieu, Ginsburg, Guérin, and Truc, 1984, partly resemble *Ornipodichnus hamoriensis*, but they differ from the Hamori species in their much wider interdigital angles between digits Ⅱ and Ⅳ, slightly larger size, and hallux impressions uncommonly shown. *Ornipodichnus hamoriensis* compares well with some of bird tracks from the Eocene Green River Formation of Utah (Moussa, 1968, Figs. 2 and 3) and some bird tracks from the Eocene Molasse deposits of France (Plaziat, 1964, Texte-Planche 2).

Ornithotarnocia lambrechti Kordos, 1983
Fig. 4-g

Figured material : A trackway (HBT_Ⅷ-L$_1$-R$_3$) comprising six footprints from the Hamori Formation, Jeju Island, Korea

Diagnosis : The same as for the ichnogenus *Ornithotarnocia* (Kordos, 1983)

Description : Bird tracks comprise impressions of a central digit (Ⅲ) and slightly curved lateral digits (Ⅱ and Ⅳ). Pes lengths are 17 to 18 mm and widths are 23 to 24 mm. Central digit (Ⅲ) is longest, 14 mm long. Lateral digits (Ⅱ and Ⅳ) are slightly curved. Thickness of digit is about 4.5 mm in average (HBT_Ⅷ). Interdigital angles between digits Ⅱ and Ⅲ and between digits Ⅲ and Ⅳ are about 50° and 70° respectively. Impressions of hallux and web are not observed.

Remarks : Three tracks are similar in general outline to holotype specimen of *Ornithotarnocia lambrechti* Kordos, 1983 (Kordos, 1983, Fig. 1-9 and 10), but they differ from type specimen in their smaller size.

Roepichnus jejuensis ichnosp. nov.
Fig. 4-h

Holotype : HBT_Ⅳ-R$_1$, brownish shale bed of the Hamori Formation, about 90 cm from the base of the measured section.

Paratype : HBT_Ⅳ-L$_2$, same as Holotype.

Deriviation of name : After Jeju Island, site of the footprints discovery, with reference to the *Roepichnus* from Jeju Island, Korea.

Diagnosis : Tetradactyl avian tracks comprising pes with impression of phalange joint nodes and curving outer digits; digits terminate in claws; hallux directed backward, short, terminate in claws; interdigital angles about 110°; full interdigital web impressions variably preserved.

Description : *Roepichnus* tracks comprising impressions of a straight central digit (Ⅲ) and curved lateral digits (Ⅱ and Ⅳ). Pes lengths are 71 mm and widths are 72 mm in average. Some digit impressions display faint nodes at phalage joints, terminating in claw points. Central anterior digit (Ⅲ) is longest, 71 mm long in average. Curved medial and lateral digits (Ⅱ and Ⅳ) are nearly equal in length, 57 mm and 60 mm in average. Angle of divergence of the medial and lateral digits (Ⅱ and Ⅳ) are nearly consistent, with spans of 107° in average. Posterior digit or hallux (Ⅰ) are well preserved and directed backwards the mid-line of track, where it comprises a short point depression. Full web impressions are observed with sharp eyes.

One trackway observed is 434 mm in length and comprises six individual prints. Pace, stride, pace angulation, and pace width of trackway are 118 mm, 107 mm, 75°, and 77 mm in average respectively.

Remarks : *Roepichnus jejuensis* is close in overall form to *Anatipeda anas* Panin and Avram, 1962, as redescribed by Sarjeant and Langston (1994), but it is distinguished by its phalange nodes, hallux impressions, wider angles of interdigital span (Ⅱ and Ⅳ), and hallux impressions directed backwards the mid-line of track. This species is also close to *Prebyorniformipes feducci* described

by Yang et al. (1995), but this differs in its much smaller size, absence of a pronounced hallux print, and its less prominent claws impressions.

Roepichnus jejuensis is distinguished from *Uhangrichnus chuni* Yang, Lockley, Greben, Erickson, and Lim, 1995 described from the Late Cretaceous of South Korea by its distinct hallux impressions, reduced webbing print with distinct concave margin. It is also similar in general outline to *Hwangsanipes choughi* Yang, Lockley, Greben, Erickson, and Lim, 1995 described from the Late Cretaceous of South Korea (Yang et al., 1995), but, it is distinguished from it by its fully developed web and narrow interdigital angle between digits Ⅱ and Ⅳ.

Roepichnus jejuensis is similar in overall form to *R. grahami* Doyle, Wood, and George, 2000, described from the Late Miocene Sorbas Member of the Sorbas Basin, southeast Spain (Doyle et al., 2000). This species is, however, distinguished from *R. grahami* by its indistinct phalange joint nodes, prominent hallux impressions, larger size, and much wider interdigital angles between digit Ⅱ and Ⅳ.

This species is similar in overall size to *Avipeda* ichnosp. E very briefly described from the Miocene Copper Canyon Formation of Death Valley National Monument, California (Scrivner and Bottjer, 1986). However it is different from *Avipeda* ichnosp. E by its unequal length of digits Ⅱ (or Ⅳ) and Ⅲ, prominent claw impressions, full interdigital web impressions, and curved outer digits (Ⅱ and Ⅳ). Webbed footprints (Form D) from the Oligocene sediments of Agramunt, Spain (Casanovas-Caldellas and Santaffe-Llopis, 1982) are similar in form to *Avipeda* ichnosp. E from Copper Canyon Formation with exception of its small size.

Very well preserved webbed footprints reported from the Lower Oligocene formation of northern Spain (de Raaf et al., 1965) are similar in size to *Roepichnus jejuensis*, but it is distinguished from this species by impressions of longer central digit (Ⅲ), partial web impressions, and much wider interdigital angle between digits Ⅱ and Ⅳ. Goose-like tracks from the Pliocene Bidahochi Formation of Arizona (Breed, 1973) are nearly similar to specimens from Spain (de Raaf et al., 1965) except their less prominent central digit (Ⅲ). Goose footprints from the Pliocene mud flat of Moraga Valley, California (Miller and Aschley, 1934) are very similar in overall size and form to *Roepichnus jejuensis*. Bird tracks, superficially similar to tracks of *Presbyornis*, reported from the Paleocene Fort Unit Formation, Wyoming (Johnson, 1986) is distinguished from *Roepichnus jejuensis* by its much less developed webbing impression. Miller and Ashley (1934) regarded that footprints like *Roepichnus jejuensis* were produced by geese.
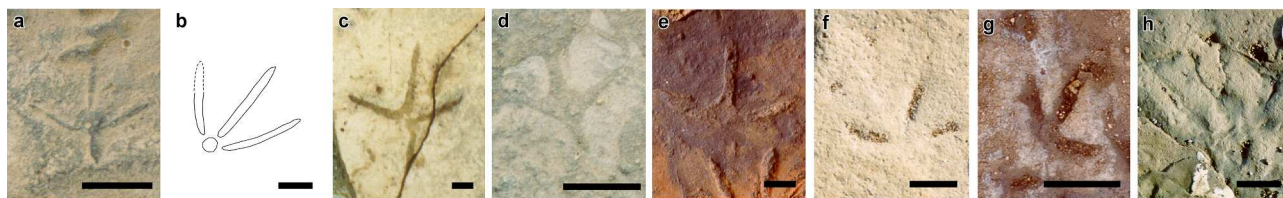

Fig. 4. Avian footprints from the Hamori Formation. a: *Ardeipeda* ichnosp., b: *Avipeda* ichnosp. c: *Gruipeda koreanensis* ichnosp. nov., d: *Ignotornis* ichnosp., e: *Koreanornipodichnus cheongi* ichnogen. et ichnosp. nov., f: *Ornipodichnus hamoriensis* ichnogen. et ichnosp. nov., g: *Ornithotarnocia lambrechti* Kordos, 1983, h: *Roepichnus jejuensis* ichnosp. nov. Scale bars in all figures are 20 mm

Other Trace Fossils

In addition to vertebrate footprints, diverse trace fossils and body fossils are found from the Hamori Formation of Jeju Island. They are briefly herein described.

Fish trails

Undichna ichnosp. (Fig. 5)

Two specimens compared with fish trails are occurred. They are sinusoidal to irregular grooves assignable to *Undichna* ichnosp. Species of *Undichna* have been previously reported from the Paleozoic and Mesozoic strata
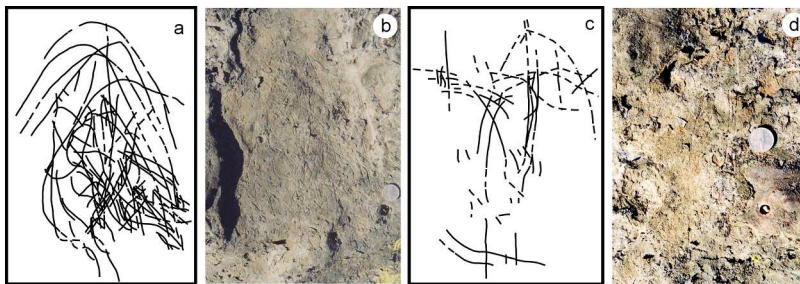

Fig. 5. *Undichna* ichnosp.. Coins in all figures are 23 mm

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(Gibert et al., 1999; Trewin, 2000).

Invertebrate trace fossils

Arenicolites ichnosp. type A (Fig. 6-a)

Vertical U-tubes without a sprite preserved in endorelief in the coarse-grained sandstone. Length of U-tube is up to 38 mm, width up to 13 mm. Tube diameter is about 1.2 mm. Funnel-shaped apertures and wall-lining are not observed. U-plane sections are somewhat irregular. *Arenicolites* is considered the dwelling and feeding burrow of suspension-feeding (particularly polychaete) annelids (Hakes, 1976) or crustacean like organisms (Goldring, 1962).

Arenicolites ichnosp. type B (Fig. 6-b, c)

Vertical U-tubes without a sprite preserved in endorelief in the coarse-grained sandstone. Length, width and tube diameter of U-tube is similar to *A.* ichnosp. type A. Funnel-shaped apertures and wall-lining are not observed. U-plane sections are somewhat irregular. The base part of U-tube is curved and gradually parallel to bedding plane. Vertical U-tubes make a right angle with the base part of U-tube.

Cochlichnus anguineus Hitchcock, 1858 (Fig. 6-d)

Regularly meandering, small horizontal burrows resembling sine curves. Specimen preserved as unlined, sinusoidal burrow, 0.1 to 0.3 mm in diameter, in convex hyporelief and concave epirelief. Amplitude is 0.9 to 1.7 mm and wavelength 2.6 to 4.2 mm. *Cochlichnus* has been found in marine and nonmarine environments (Keighley and Pickerill, 1997). A vermiform animal is the most typically inferred producer of these traces (e.g., nematodes, as observed by Moussa, 1970, and Metz, 1998; or annelids suggested by Hakes, 1976), though Metz (1992) observed that short-bodied organisms such as insects can also produce such structures.

Diplocraterion parallelum Torell, 1870 (Fig. 6-e)

Vertical U-shaped spreiten burrow preserved in endorelief. Burrows are straight to steep and can be observed either as dumb-bell in epirelief or U-tubes in vertical section, or both. Burrows are 2-3 mm wide, 3-5 mm deep and up to 1 mm thick. Spreite is typically well developed, protrusive. Distance between the apertures is generally constant along the burrow depth, resulting in parallel arms. *Diplocraterion* is believed to represent the Domichnion of polychaete annelids (Arkell, 1939), crustaceans (Fürsich and Schmidt-Kittler, 1980; Runnegar, 1982) or other unrecognized suspension feeders (Goldring, 1962; Fürsich, 1974).

Helminthopsis hieroglyphica Heer in Mailland, 1887 (Fig. 6-f)

Unbranched, irregularly winding, horizontal burrows, preserved in concave epirelief and convex hyporelief. Diameter of burrow is, nearly constant within a burrow, up to 2 mm. *Helminthopsis* is generally regarded as having been produced by polychaete annelids and possibly priapulids (Fillion and Pickerill, 1990).

Lophoctenium ichnosp. (Fig. 6-g)

Concave epirelief burrow. Burrow consists of nearly straight parts and curved parts. Straight parts consist of two to four, continuous to discontiuous, furrows and are up to 17 mm in width. Curved parts are composed of continuous to discontinuous, concentric furrows strongly curved, and are up to 47 mm in width. Burrows in the sinuous parts are up to ten at maximum. Total length of a burrows observed is about 550 mm. The ichnogenus *Lophoctenium* is a deposit-feeder trace fossil consisting of one or more bundles of radiating grooves produced by the repeated probings in the sediment by a semi-stationary animal (Fu, 1991).

Palaeophycus tubularis Hall, 1847 (Fig. 6-h)

Subcylindrical, straight to curved, horizontal to inclined, unbranched burrows preserved in convex epirelief. Diameter of burrow ranges from 6 to 11 mm. *Palaeophycus* is interpreted as a dwelling structure(domichnia) of a suspension feeder or predaceous organism (Pemberton and Frey, 1982).

Protovirgularia dichotoma McCoy, 1850 (Fig. 6-i)

Unbranched, keel-like trail, mostly straight of slightly curved, consisting of lateral chevron

markings opening in the direction of movement of the protruding organism. The specimen, preserved in concave epirelief, is 100 mm in length and 14 mm in width. Central furrow is 1 mm in width, discontinuous. Wedge-shaped appendages, 1-1.5 mm thick, emanating from a central furrow. Seilacher and Seilacher(1994) convincingly demonstrated that the ichnotaxon is produced by bivalves burrowing in, or crawling on, soft substrates.

Skolithos linearis Haldemann, 1840 (Fig. 6-j)

Straight, nearly vertical, unbranched cylindrical burrows preserved in endorelief. Burrows range from 3 to 6 mm in diameter and up to 235 mm long. Concentric rims, up to 100 mm in diameter, are characteristically developed around one to five adjacent burrows. *Skolithos* is generally regarded as the dwelling and feeding burrows of annelids or phoronids (Alpert, 1974).

Spongeliomorpha ichnosp. (Fig. 6-k)

Cylindrical, curved burrow with distinctly thick wall. Burrow is 420 mm in diameter. Diameter of wall is 3 mm. The outer surface of burrow is covered by small, irregular ridges. The fine and sharp rhombohedral ridges of the burrow surface are interpreted as scratch marks produced by crustaceans (Kennedy, 1967). This structures are clearly produced during firmground surfaces (Fürsich, 1975; Bromley and Allouc, 1992).

Taenidium satanassi D'Alessandro and Bromley, 1987 (Fig. 6-l)

Straight to curved, horizontal unwalled, meniscate, backfilled burrows preserved in concave epirelief. Menisci consist of alternating weakly arcuate packets of sediment. Burrows are 7 to 8 mm in width, up to 71 mm long. Menisci thickness varies from 3 to 6 mm. The fill is typically darker in color than the host sediment and finer grain size. *Taenidium* is considered to be produced by arthropods (e.g., Keighley and Pickerill, 1997) and bivalves (e.g., Pryor, 1967).

Thalassinoides paradoxicus (Woodward 1830) (Fig. 6-m)

Irregularly branched, smooth, cylindrical boxwork burrows preserved in endorelief. Diameter of burrow range from 25 to 140 mm. Burrows are enlarged at points of bifurcation and almost Y-shaped branchs. Burrow walls are 2 to 3 mm in diameter. T. paradoxicus has been considered to be formed in firmground (Myrow, 1995).

Thalassinoides suevicus (Rieth, 1932) (Fig. 6-n)

Predominantly horizontal, more or less regularly branched, cylindrical burrow system preserved in endorelief. Y-shaped branchs are common. Burrows are 3 to 54 mm in diameter, distinctively enlarged at points of bifurcation. *Thalassinoides* is a face-crossing trace fossil, most typical of shallow-marine environment and it is produced mainly by crustaceans (e.g., Frey et al., 1984).

Ophiomorpha nodusa Lundgren, 1891 (Fig. 6-o)

Cylindrical burrow with straight to slightly curved, horizontal to slightly oblique. In place pelletoidal exterior is developed. Agglutinated pelletoidal sediments are irregular in shape. Burrow bifurcation is not observed. Burrow is about 23 mm in diameter and 320 mm in length. Individual pellets range from 3 to 5 mm in diameter and generally considered to be a wall-supporting structure that prevents collapse of unconsolidated sediment during and after burrow construction (Asgaard and Bromley, 1974; Ekdale et al., 1984; Bromley, 1996)

Arthropod trackway type A (Fig. 6-p)

The trackway consist of a single keel-like central ridge and two rows of imprints. A single keel-like median ridge is similar to *Protovirgularia* with lateral, generally paired and bilaterally symmetrical, narrow wedge-shaped appendages. Patterns of lateral appendages arrangement on median ridge are alternate. Median ridge is 4 mm in width and 180 mm in length. The number of imprints in a series is only one and make a nearly right angle with median ridge. The imprints range from 3 to 4 mm in length and less than 1 mm in width. Preserved as convex epirelief.

Arthropod trackway type B (Fig. 6-q, r, s)

Trackway preserved in convex hyporelief or concave epirelief. Trackway, slightly curved, characteristically comprises series of seed-like oblong imprints, tapering to sharp points at forward

end and rounded to obtuse points at backward end. Mid line is not observed. Each imprint series consists of three imprints. Trackway is 16 mm in width. Each imprint is up to 8 mm in length, up to 2.5 mm in width. Right imprint in each imprint series is more slender than the other two imprints. Distances between left imprint and central imprint and between right and central imprints in each imprint series are 6-8 mm and 4-6 mm respectively. This trackway is considered to be attributed to crab-like arthropod. Bivalves and gastropods, small crabs, rhizolith and plants assigned to *Magnolia* sp. are also found.
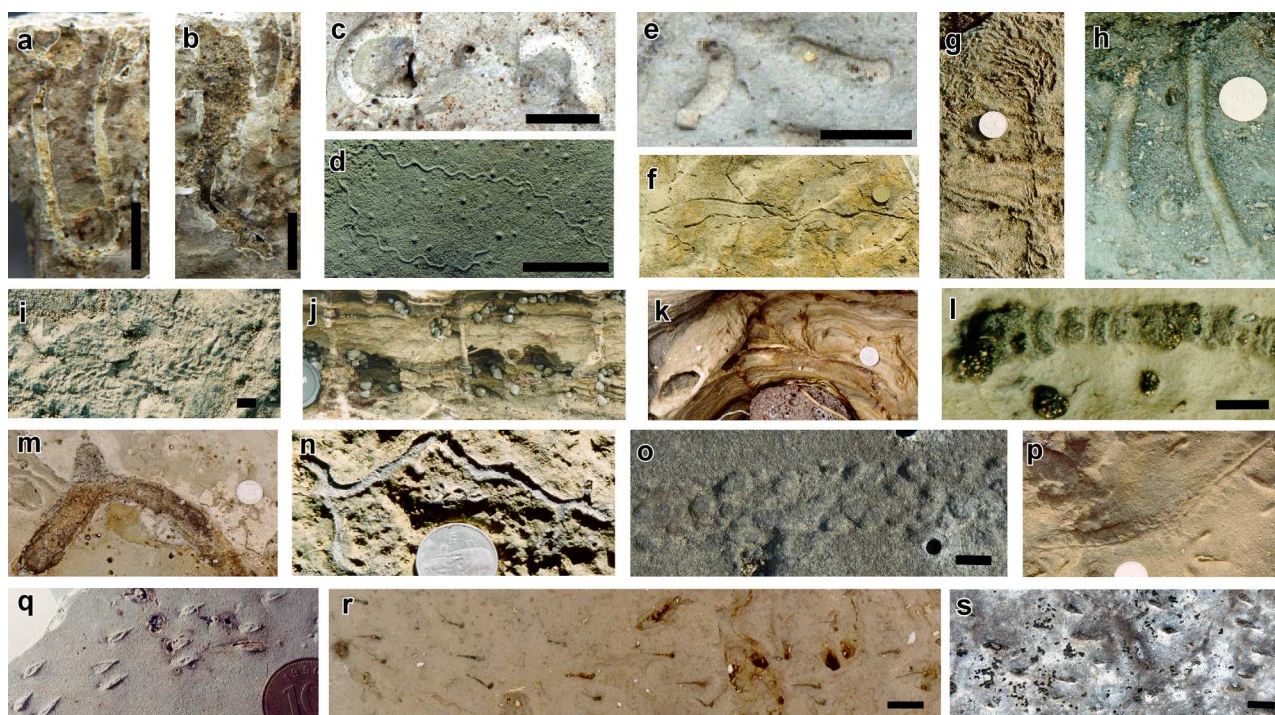

Fig. 6. Invertebrate trace fossils from the Hamori Formation. a: *Arenicolites* ichnosp. type A, b, c: *Arenicolites* ichnosp. type B, , d: *Cochlichnus anguineus*, e: *Diplocraterion parallelum*, f: *Helminthopsis hieroglyphica*, g: *Lophoctenium* ichnosp., h: *Palaeophycus tubularis*, i: *Protovirgularia dichotoma*,, j: *Skolithos linearis*, k: *Spongeliomorpha* ichnosp., l: *Taenidium barretti*, m: *Thalassinoides paradoxicus* n: *Thalassinoides suevicus*, o: *Ophiomorpha nodusa*, p: Arthropod trackway type A, q, r, s : Arthropod trackway type B. Coins, camera caps and scale bars in all figures are 23 mm, 67 mm, and 10 mm, respectively.

DISCUSSION
Depositional Environments

In the study area, the ichnofaunas are represented by one ichnospecies of fodinichnia and fodinichnia/pascichnia, three pascichnia and repichnia, and eight domichnia. These trace fossils are classified by the feeding pattern to deposit- and suspension-feeding.

A vertical domichnia are the most abundant and widely occurs in the study area. Domichnia, like *Arenicolites* and *Skolithos*, have been interpreted to be produced in the high-energy condition and *Thalassinoides paradoxicus* has been considered to be formed in firmground (Myrow, 1995) and *T. suevicus* is typical from in soft ground (Myrow, 1995). The coexistance of both deposit- and suspension-feeding trace fossils suggests the presence of sufficient nutrient levels and adequate oxygenation (Han and Pickerill, 1994).

Sedimentary structures including mud cracks, Runzelmarken, and small wave ripple marks occurred on the bedding surface of laminated mudstone to shale and fine- to coarse-grained sandstone associated with diverse vertebrate footprints and invertebrate trace fossils may indicate shallow shoreline environment, especially semi-closed lagoon or intertidal flat setting, existed at the time when the tracks were made. Each footprints bearing surface represents a period of submergence followed by a period of emergence. Footprints were probably formed on this emergent or shallowly submergent muddy to sandy sediments which were partially dry or firm enough to walk upon without miring.

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Paleontological Significance

As shown in the previous section, a total of fourteen ichnospecies of vertebrate footprints, one of fish trail, and sixteen of invertebrate trace fossils were recognized from the Hamori Formation of Jeju Island, Korea (Table 1). They are divided into footprints of hominids, avian, artiodactyla, proboscidean(?), carnivore(?), and unidentified vertebrate footprints type Ⅰ and Ⅱ, and traces of fishes and invertebrate animals. The described footprints are footprints of deer-like artiodactyl animal, *Bifidis jejuensis* ichnosp. nov., and footprints of avian, *Ardeipeda* ichnosp., *Avipeda* ichnosp., *Ignotornis* ichnosp., *Gruipeda koreanensis* ichnosp. nov., *Koreanornipodichnus cheongi* ichnogen. et ichnosp. nov., *Ornipodichnus hamoriensis* ichnogen. et ichnosp. nov., *Ornithotarnocia lambrechti* Kordos, 1983, and *Roepichnus jejuensis* ichnosp. nov.

Table 1. Occurrence of fossils in the study area.

Classification				Sites	Number
Trace Fossil	Invertebrate			Numerous	Numerous
	Vertebrate	Fish		2	2
		Avian		10	200<
		Mammal	Hominid	8	140<
			Artiodactyla	15	1,000<
			Proboscidean(?)	2	100<
			Carnivore(?)	4	10<
			Unidentified Footprint Ⅰ	1	8
			Unidentified Footprint Ⅱ	2	17
Body Fossil	Arthropod	Crustacea		1	7
	Plant	Leaf		2	2
	Mollusk	Gastropod		1	4
		Bivalve		1	1

Vertebrate footprints recognized in the Pleistocene Hamori Formation are significant in the point of their diversity and abundance, and pausity of previous similar records. Their diversity and abundance may only be comparable with those of Pliocene Laetoli in Tanzania (Leakey and Hay, 1979), Eocene deposits of Trans-Pecos Texas (Sarjeant and Langston, 1994) and Late Miocene Copper Canyon Formation of California (Scrivner and Bottjer, 1986), though many reports have documented records of vertebrate footprints from the Cenozoic strata (e.g. references in Scrivener and Bottjer, 1986).

So far as the authors' knowledge, fossil hominid footprints have rarely been known, though hominid footprints have frequently reported from the Holocene deposits (e.g. Haberland and Grebe, 1957; Bryan, 1973; Politis and Bayón, 1995; Belperio and Fotheringham, 1990; Robert et al., 1996; Aldhouse-Green et al., 1992; Allen, 1997; Frey and Pemberton, 1986; Clottes and Simonet, 1972). Fossil hominid footprints have been previously reported from the Late Paleolithic Grottes of Central France (Vallois, 1931), Late Pleistocene deposits of Nahoon Point in South Africa (Mountain, 1966), Middle Pliocene sediments of Laetoli in Tanzania (Leakey and Hay, 1979; Day and Wickens, 1980; Hay and Leakey, 1982), Pleistocene Koobi Fora Formation of Kenya (Behrensmeyer and Laporte, 1981), Pleistocene deposits at Oro Grande in the southwestern part of the Mojave Desert (Rector, 1999), and Middle Pleistocene deposits of northwest Campania in Italy (Mietto et al., 2003).

Fossil footprints of birds and deer-like artiodactyls have been frequently reported from the Cenozoic strata (e.g. references in Scrivner and Bottjer, 1986; Sarjeant and Langston, 1994; Doyle et al., 2000). In addition to numerous hominid and mammalian footprints and diverse and abundant invertebrate trace fossils, eight ichnospecies herein erected from the birds footprints may be noteworthy in the point of their diversity compared with previously known reports.

Paleoecological Significance

According to Cohen et al. (1993) who studied modern mammal and bird tracks from the Lake Manyara of Tanzania, most species of vertebrate leave a track record and common species leave abundant tracks, although numbers of trackways are not proportioned to numbers of individuals. Numerous vertebrate footprints may allow to shed light on the composition of the animal community (Lockley and Hunt, 1995). Examination of footprints abundance from the Hamori Formation shows that deer-like artiodactyl footprints are most common and footprints attributed to birds, hominids, proboscidean(?), and carnivore(?) are less common (Table 1). The animal community based on the track census data drawn from over one thousand occurrence of footprints may somewhat

comparable with that of the Miocene Copper Canyon Formation (Scrivner and Bottjer, 1986). Most of these probable trace makers are considered to be occasional and habitual visitors to the shoreline environment on the basis of dominantly shoreline-parallel distribution of the footprints.

Diverse and abundant vertebrate footprints and invertebrate trace fossils associated with body fossils including gastropods, bivalves, crabs, and plants may allow to reconstruct a food-chain pyramid, a paleocommunity of the Hamori fauna, at the time when diverse trace making organisms live in the shoreline environment. As shown in Fig. 7, intelligent and omnivorous hominids, probably *Homo sapiens*, may be positioned on the top of the food-chain pyramid. The second top position may be occupied by the carnivore(?), and then vertebrates including herbivorous artiodactyla, proboscidena(?), and insect- and fish-eating birds who visited the shoreline environment probably for hunting fishes, molluscs, the insects, or worms, eating plants, or drinking saline water as food material or physiological need. Subsequently, mulluscs, fishes, and crabs located in the fourth position fed insects or worms positioned at the lower most level which could be mainly inferred from the possible producers of sixteen invertebrate trace fossils.

The reconstruction of paleoecological view of the Pleistocene Hamori Formation estimated on the basis of occurrence of vertebrate and invertebrate trace fossils is shown in Fig. 8. A possible modern analog partly compared to the diverse vertebrate and invertebrate community surrounding the ancient Hamori shoreline is that in Georgia barrier islands where more than 100 species of potential trace makers were identified on the basis of diverse vertebrate trace fossils (Frey and Pemberton, 1986).
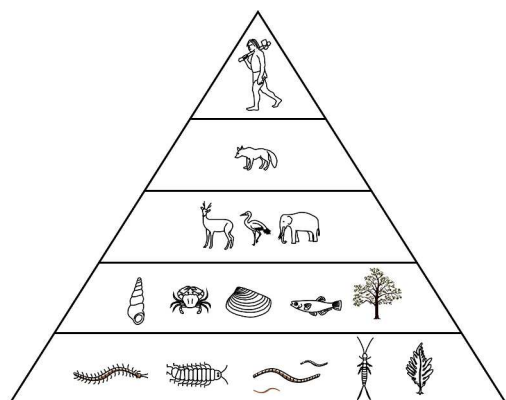

Fig. 7. Food chain pyramid inferred from the footprints of vertebrates, invertebrate trace fossils and body fossils.
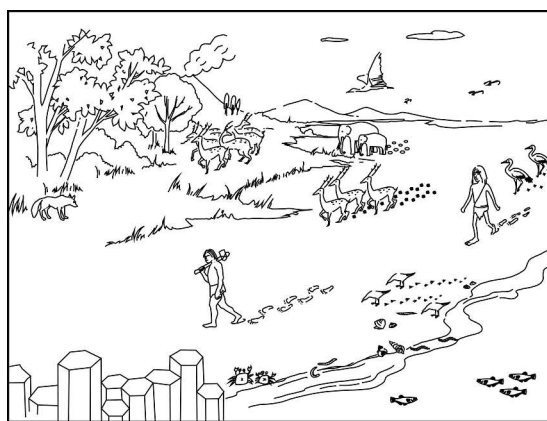

Fig. 8. Paleoecological view reconstructed by footprints of vertebrates, invertebrate trace fossils and body fossils.

CONCLUSION

1. Two type vertebrate footprints including eight ichnogenera and ichnospecies of avian footprints and one ichnogenus and ichnospecies of artiodactyla footprints, one ichnospecies of fish trail, and thirteen ichnogenera and sixteen ichnospecies of invertebrate trace fossils were systematically described from the Hamori Formation, Jeju Island. They are *Bifidis jejuensis* ichnosp. nov. (artiodactyla), *Undichna* ichnosp. (fish), *Ardeipeda* ichnosp., *Avipeda* ichnosp., *Gruipeda koreanesis* ichnosp. nov., *Ignotornis* ichnosp., *Koreanornipodichnus cheongi* ichnogen. et ichnosp. nov., *Ornipodichnus hamoriensis* ichnogen. et ichnosp. nov., *Ornithotarnocia lambrechti* Kordos, 1983, *Roepichnus jejuensis* ichnosp. nov. (avian), *Arenicolites* ichnosp. type A., *A.* ichnosp. type B, *Cochlichnus anguineus* Hitchcock, 1858, *Diplocraterion parallelum* Torell, 1870, *Helminthopsis hieroglyphica* Heer in Mailland, 1887, *Lophoctenium* ichnosp., *Palaeophycus tubularis* Hall, 1847, *Protovirgularia dichtoma* McCoy, 1850, *Skolithos linearis* Haldmann, 1840, *Spongeliomorpha* ichnosp., *Taenidium satanassi* D'Alessandro and Bromley, 1987, *Thalassinoides paradoxicus* (Woodward, 1830), *T. suevicus* (Reith, 1932), *Ophiomorpha nodusa* Lundgren, 1891, Arthropod trackway type A, and Arthropod trackway type B.

2. The hominid, proboscidean(?), and carnivore(?) footprints, and unidentified footprints type I and II were occurred.

3. The Hamori Formation of the fossil locality seem to deposit in shallow shore line environment,

especially semi-closed lagoon or intertidal flat setting.

4. By examination of footprints abundance, deer-like artiodactyla footprints are most common and footprints attributed to birds, hominids, proboscidean(?) and carnivore(?) are less common in the Hamori Formation.

5. By analyzing diversity and abundance of vertebrate footprints and invertebrate trace fossils associated with body fossils including gastropods, bivalves, crabs and plants, the paleocommunity and paleoecology of the Hamori fauna were reconstructed.

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