Vertebrate footprints from the Agha Jari Formation (late Miocene–Pliocene), Zagros Mountains, and a review of the Cenozoic vertebrate ichnites in the Persian Gulf region

Nasralloh Abbassi & Hooshang Dashtban

Numerous vertebrate footprints have been found in the Konar Takhteh area (north Bushehr, north Persian Gulf) in the Agha Jari Formation. Mammal footprints are attributed to artiodactyls and have been assigned to *Pecoripeda gazella*. Avian footprints have been assigned to *Koreanaornis hamanensis*, and *Persiavipes gulfi* ichnogen. nov. and ichnosp. nov. *Koreanaornis hamanensis* has small tetradactyl footprints with slender digit imprints. *Persiavipes gulfi* has tetradactyl, semipalmate footprints, with distinctive, short interdigital webbing in the three anterior digits. Its backward rim is round, and the digit I imprint is well developed. In addition to the Konar Takhteh tracksite, there are other six tracksites in the Persian Gulf area, from Paleogene and Neogene deposits in Iran, Iraq, Oman, and UAE. These footprints have been attributed to large proboscideans, medium to small artiodactyls and very large to small shore birds. The ichnodiversity from northern regions of the Persian Gulf is higher than from the southern parts. In the same way, the ichnodiversity increases from the interior realm of the Arabian Peninsula to Central Iran, because there are no data about Cenozoic vertebrate ichnites in interior parts of Arabian Peninsula. Ichnodiversity in Central Iran, however, includes 24 ichnotaxa, and it may show higher biodiversity in the central Iranian Plateau relative to adjacent areas. • Key words: footprints, mammal, bird, Cenozoic, Zagros Mountains, Persian Gulf.

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Vertebrate ichnology of the Cenozoic non-marine sediments of the Iranian and Arabian plates is important for the reconstruction of terrestrial vertebrate distribution in the Afro-Eurasian continents after the subduction of Neo-Tethys. A part of this importance is related to Cenozoic vertebrate migrations between Afro-Eurasian territories via the Iranian corridor (Hopkins 1959, Steininger *et al.* 1985, Tchernov 1992, Vrba 1992). The Iranian land bridge, however, may have been limited by natural barriers such as the Zagros Mountains, resulting in endemic realms for some species in Central Iran and the Persian Gulf region. Contrary to the body fossils, vertebrate footprints are autochthonous documents, and new data from Cenozoic vertebrate tracks from Persian Gulf region are an important aid for paleobiogeographic studies of the Middle East. In this context, the aim of this study is twofold: 1) to report a new vertebrate tracksite from the Persian Gulf region and, 2) to evaluate Cenozoic mammal and bird ichnodiversity in the Middle East. The new footprints described in this contribution are from the Agha Jari Formation (late Miocene–Pliocene) in the northwest of Konar Takhteh, Bandar-e Bushehr area, northern Persian Gulf (Fig. 1).

Geological setting and historical background

The Persian Gulf is an epicontinental margin basin surrounded by the Zagros Mountains, which form the active margin in the north and the Arabian stable foreland in the south (Purser & Seibold 1973). The oil-bearing Zagros Mountains are northwest-southeast-trending from northern Iraq to southeast Iran and have been interpreted as the active zone of the Arabia-Eurasia collision belt (Stöcklin 1968, Alavi 2004, Allen *et al.* 2006). The tectonic history of the Zagros Mountains consists of three stages, so that the stable platform stage of the southern margin of the Paleo-Tethys Ocean (early Cambrian to Permian) and Jurassic

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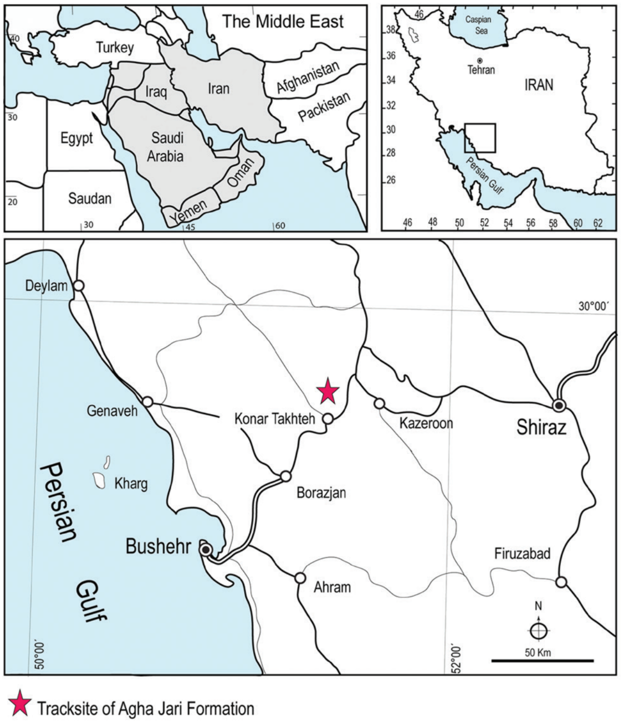

Figure 1. Location map of the track site of Konar Takhteh.

passive continental margin stage represent the first two stages (Stöcklin 1977, Koop & Stoneley 1982, Motiei 1993, Alavi 2004, Sepehr & Cosgrove 2004, Sherkati & Letouzey 2004, Agard *et al.* 2005, Mohajjel & Fergusson 2014). The final stage of Cretaceous–Recent subduction to collision basin, however, includes subsidence of the basin of Zagros accompanied by thick sedimentation during the Cretaceous and subduction of the Neo-Tethys that led to Arabian-Iranian collision (Motiei 1993, Aghanabati 2004, Alavi 2004). This stage was ended by a post-collision transgressive sequence of the Fars Group (the Gachsaran, Mishan, Agha Jari and Bakhtyari formations) during the Miocene to Pliocene, and the Zagros Basin migrated to its present position in the Persian Gulf region (Koop & Stoneley 1982, Alavi 2004). The Fars Group includes sedimentary rocks that were deposited in supratidal and sabkha environments at the base (Gachsaran Formation), marine carbonate and marl (Mishan Formation), sedimentary rocks of the coastal plain and meandering rivers (Agha Jari Formation) and, finally, conglomerate formed in a braided river environment (Bakhtyari Formation). Cenozoic rocks of the Zagros Mountains in north Iraq comprise sedimentary units otherwise like those of the Zagros Mountains, however, there are local formations. For example, the Injana Formation and Mukdadiya and Bai Hassan formations are equivalent to the Upper Fars and Bakhtyari formations, respectively (Jassim & Buday 2006) (Fig. 2).

Although the northwestern and southern parts of the Persian Gulf present relatively stable tectonic conditions, they include several structural domains, from the northwest to southeast of the Persian Gulf: Kirkuk embayment and Mesopotamian basin in Iraq, Dibdibba-Ghawar basin in the west of the Persian Gulf, Qatar arch, and the Rub' Al-Khali and Ras Al-Khaimah basins, Dibba and Oman Mountain in the southern parts (Searle *et al.* 1983, Ziegler 2001, Burberry 2015). Likewise, Cenozoic rock units of the southern parts of the Persian Gulf are the same as those of the Zagros Mountains and include the Pabdeh-Jahrum, Asmari, Lower Fars (Gachsaran) and Upper Fars (Mishan) formations in Qatar, eastern UAE and the Oman Mountains (Glennie *et al.* 1973, Searle *et al.* 1983, Ziegler 2001) (Fig. 2). There were, however, major hiatuses during the late Eocene–early to middle Miocene in the Qatar arch and the northeast of Saudi Arabia and Kuwait. In these areas, Tertiary rocks include the Umm Er Radhuma (Paleocene–lower Eocene), Rus and Dammam (Eocene), Hadrukh, Dam, Ghar, Hofuf, Lower Fars, Upper Fars (Miocene), Dibdibba and Bakhtyari (Pliocene) formations (Fig. 2). Late Miocene terrestrial sediments of the coastal area in the west of the UAE are known locally as the Baynunah Formation (Whybrow 1988, Whybrow *et al.* 1999).

There are some reports of Cenozoic vertebrate footprints from the Persian Gulf region and adjacent areas that include numerous ichnotaxa (Figs 2, 3; Tab. 1). Three reports of footprints in the Persian Gulf region are from the Zagros Mountains and others are from Cenozoic outcrops

Table 1. The list of reported Cenozoic vertebrate footprints from the Persian Gulf region.

Age	Track maker	Location	Formation	Reference
Pliocene	Shore birds	Iran	Agha Jari	Lambrecht (1938)
	Artiodactyl/shore birds	Iran	Agha Jari	This paper
	Artiodactyl/shore birds	Iraq	Mukdadiya	Karim *et al.* (2003), Abbassi *et al.* (2020), this paper
Miocene	Artiodactyl	Oman	Barzaman	Schulp *et al.* (2011)
	Proboscidean	UAE	Baynunah	Higgs *et al.* (2003), Bibi *et al.* (2012)
Eocene	Mammal/Bird	Iran	Kashkan	Yousefi Yeganeh *et al.* (2011)

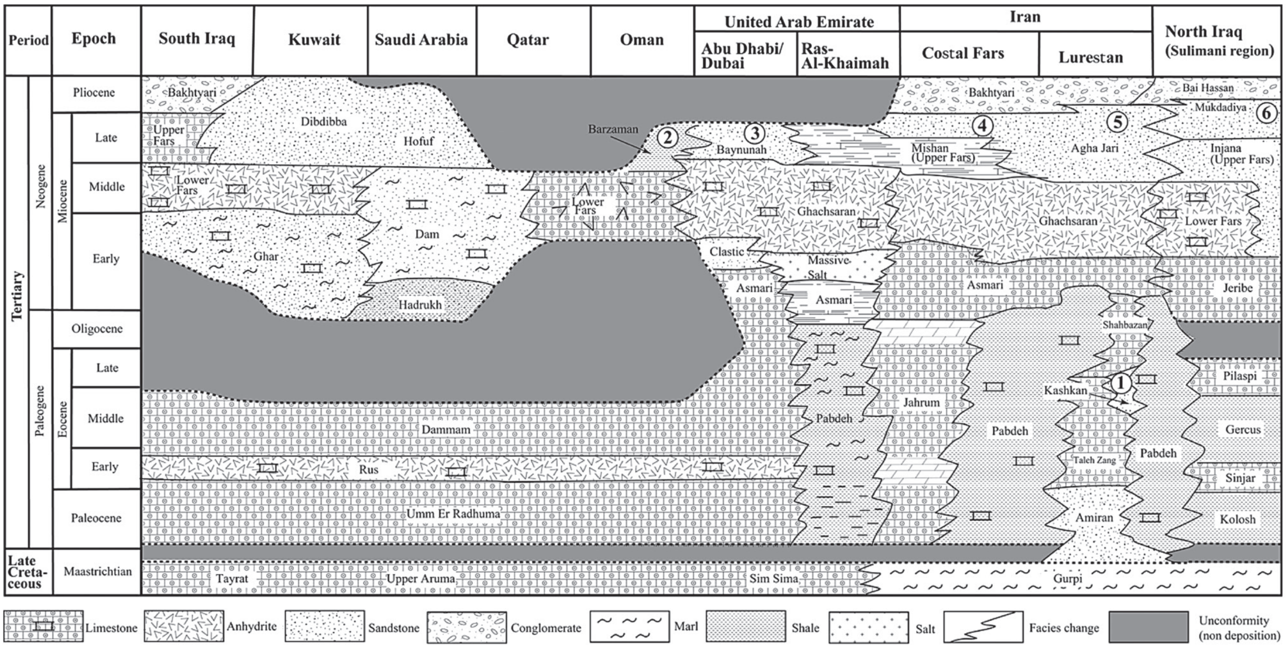

Figure 2. Stratigraphy chart of Paleogene–Neogene formations of the Persian Gulf and adjacent areas and position of the reported track sites. Modified from James & Wynd (1965), Motiei (1993), Whybrow *et al*. (1999), Alavi (2004) and Jassim & Buday (2006). Legend: 1 – bird and mammal tracks, Yousefi Yeganeh *et al*. (2011); 2 – large artiodactyl footprints, Schulp *et al*. (2011); 3 – proboscidean footprints, Bibi *et al*. (2012); 4 – mammal and bird footprints (this paper); 5 – bird footprints, Lambrecht (1938); 6 – bird and hoofed mammal tracks, Karim *et al*. (2003).

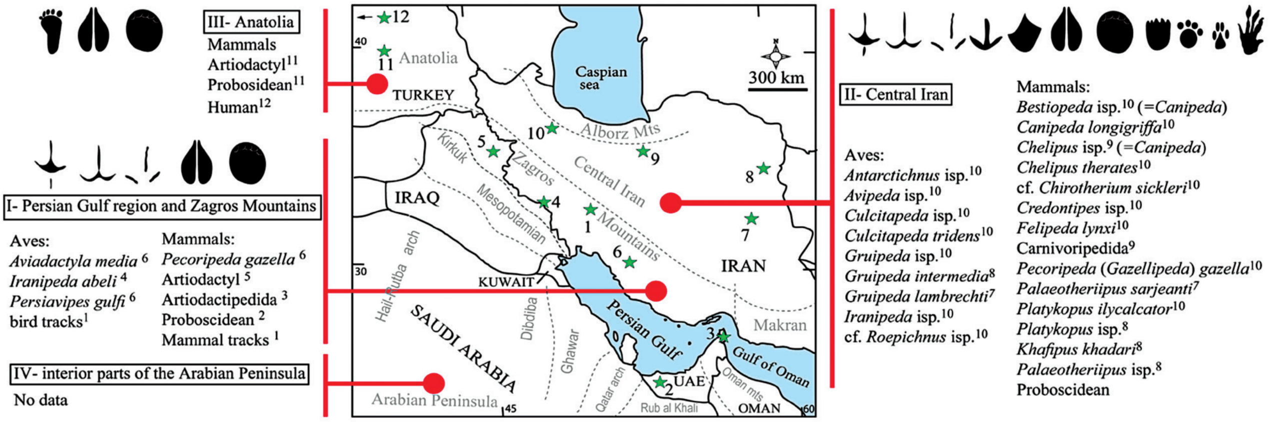

Figure 3. Distribution of reported Cenozoic vertebrate tracks in the Middle East. I – Persian Gulf region: 1 – Eocene, mammal and bird footprints, Khorram Abad area, Zagros Mountains, Yousefi Yeganeh *et al*. (2011); 2 – Miocene, proboscidean footprints, Mleisa area, United Arab Emirates, Bibi *et al*. (2012), Higgs *et al*. (2003); 3 – Miocene, artiodactyl footprints, Al Jissah, Oman, Schulp *et al*. (2011); 4 – Pliocene, shorebird footprints, *Iranipeda abeli*, Jabal Hamrin, Iran, Lambrecht (1938); 5 – Pliocene, bird and artiodactyl footprints, Chamchemal, Iraq, Karim *et al*. (2003), Abbassi *et al*. (2020); 6 – Pliocene, bird, and artiodactyl footprints, Konar Takhteh, Iran (this report). II – Central Iran: 7 – Eocene sediments, Birjand area Ataabadi & Kazaee (2004); 8 – Oligocene sediments, Khaf area, Abbassi *et al*. (2015); 9 – Upper Red Formation, Miocene, Eyvanekey, Abbassi & Amini (2008); 10 – Upper Red Formation, Miocene, Zanjan area, Abbassi & Shakeri (2005), Abbassi (2010), Alavi *et al*. (2016), Khoshyar *et al*. (2016). III – Anatolia: 11 – Karayün Formation, Oligocene, Sivas basin, Mesci *et al*. (2019); 12 – volcanite, middle Pleistocene, Çakallar Hill, west Turkey, Ozansoy (1969).

along the southern coast of the Persian Gulf, north Arabian Peninsula (locations 1 to 6 in Fig. 3).

The first report of vertebrate footprints, not only from the Zagros Mountains but also from the Middle East, is related to the Agha Jari Formation (Pliocene) from Jabal Hamrin, south Musian, Ilam province, southwest Iran (Lambrecht, 1938, Vialov, 1989, Abbassi *et al.* 2015). This footprint was called *Iranipeda abeli* (Lambrecht, 1938) (Vialov 1989) and considered as a valid name by Abbassi *et al.* (2015), although Sarjeant & Langston (1994) proposed to combine this ichnospecies under *Gruipeda*. Based on the location of this footprint, it can be inferred that it has been sampled from the upper layers of the Agha Jari Formation, known as the Lahbari Member, and Pliocene in age (Setudehnia & Perry 1967). Yousefi Yegeneh *et al.* (2011) reported bird and mammal tracks with a short description from the Kashkan Formation (Eocene) in the Khorram Abad area, in the north-central Zagros Mountains. Abundant tetradactyl large bird footprints and hoofed mammal footprints have been reported from the Mukdadiya Formation of the Chamchemal area in north Iraq, northwest Zagros Mountains (Karim *et al.* 2003, Abbassi *et al.* 2020). This formation correlates to the lower Bakhtyari Formation, and the footprints are Pliocene in age (Karim *et al.* 2003). Numerous tracks have been discovered from the Baynunah Formation in the Mleisa area, west Abu Dhabi Emirate, southern Persian Gulf (Higgs *et al.* 2003, Bibi *et al.* 2012). These footprints are late Miocene in age and have been made by proboscideans. One poorly preserved trackway of a large artiodactyl has been found in the restricted and collapsed cave ceiling of the coastal cliff of Al Jissah on the eastern shore of the Musandam Peninsula in the far north of Oman. This trackway was found in the middle Miocene or younger sediments of the Barzaman Formation (Schulp *et al.* 2011).

Agha Jari Formation

The studied vertebrate footprints were sampled from the Agha Jari Formation (Fig. 4). This rock unit consists of an alternation of grey, brown to red beds of calcareous mudstones and sandstones with gypsum veins, and has an approximate thickness of 3000 m (James & Wynd 1965, Stöcklin & Setudehnia 1991). The type section of the formation was measured in the Agha Jari oil field in the northern Persian Gulf (James & Wynd 1965, Motiei 1993, Ghazban & Motiei 2009). The Mukdadiya Formation in North Iraq, Dibdiba Formation in south Iraq, and the Hofuf Formation in Kuwait and Saudi Arabia have a same stratigraphic position as the Agha Jari Formation (Motiei 1993) (Fig. 2). Notwithstanding the extensive outcrops of the Agha Jari Formation in the Zagros Mountains, there are no comprehensive studies on the depositional environment of this rock unit. Continental to shallow marine conditions generally have reported for the depositional environments of the Agha Jari Formation (Motiei 1993, Ghazban & Motiei 2009), and continental conditions are confirmed by the occurrence of terrestrial vertebrate footprints. The lithofacies of the Agha Jari Formation changes from mostly continental clastic sediments in the Dezful Embayment to marine characteristics in the Coastal Fars (Bahrami 2009, Pirouz *et al.* 2011, Sahraeyan & Bahrami 2012). The Agha Jari Formation is late Miocene to Pliocene in age base on charophytes, microfauna, such as foraminifers and ostracods, and macrofauna such as bivalves (James & Wynd 1965). The uppermost layers of the formation change to weathered gypsum-veined siltstone, silty marl and sandstone and gypsum intercalations in the northwest Zagros Mountains and are known as the Lahbari Member (Pliocene) (James & Wynd 1965). These layers are green to gray, and climbing and oscillation ripple marks, chevron cross-bedding and invertebrate trace fossils are common (Fig. 4).

Study method and materials

The study of the Agha Jari Formation footprints includes two main phases of field collecting and detailed studies in the laboratory. Specimens were sampled from the Konar Takhteh area at coordinate 29° 39′ 13″ N, 51° 20′ 04″ E (Fig. 1) and consist of six slabs of bird footprints and two large slabs of hoofed mammal footprints. These samples were deposited in the Qeshm Geopark Museum (QGM, registered by the Global Network of Geoparks (GGN), Hormozgan Province, Iran) with the collection number QGM-2888-S1to QGM-2888-S8, and two plaster molds were prepared from the bird footprint samples numbered QGM-2888-S1 and QGM-2888-S4, and preserved with the collection numbers IFMI-575 and IFMI-576, respectively (Ichnofossil Museum of Iran, IFMI; in Zanjan Province, Iran, under construction). We used known methods for studying the morphology of bird and mammal footprints (Leonardi 1987, De Valais & Melchor 2008). The measurement taken on footprints include stride (S) and pace (P) length, footprint width (FW), footprint length (FL), plus and without digit I (FL + I and FL − I), length of digits (DL) and angle between digits II–III (= $\alpha1$), III–IV (= $\alpha2$) and II–IV (= $\alpha3$). If the lateral digit traces are straight, the angle between digits is known as a similar measure of digit divarication, but if the digits are curved (*i.e.*, digits II and IV form curved traces), then the measurement can become much more subjective (Camens & Worthy 2019). Figure 5 shows the manner of measurements of the bird footprint morphology (De Valais & Melchor 2008). Some measurements, such as digital angles and the ratio of FL/FW, were useful for ichnotaxonomic determinations of the webbed bird or artiodactyl footprints. Photographic analysis and sketches of the outlines of the footprints were useful in visualization for the morphology of studied footprints. Digital three-dimensional photos of bird footprints were obtained by high-resolution digital photogrammetry, according to a standard protocol for ichnological studies (Falkingham 2012, Falkingham *et al.* 2018). A Canon EOS-M2 photographic camera and the software packages Agisoft PhotoScan Professional (Educational License), Cloud Compare, were used for this method.

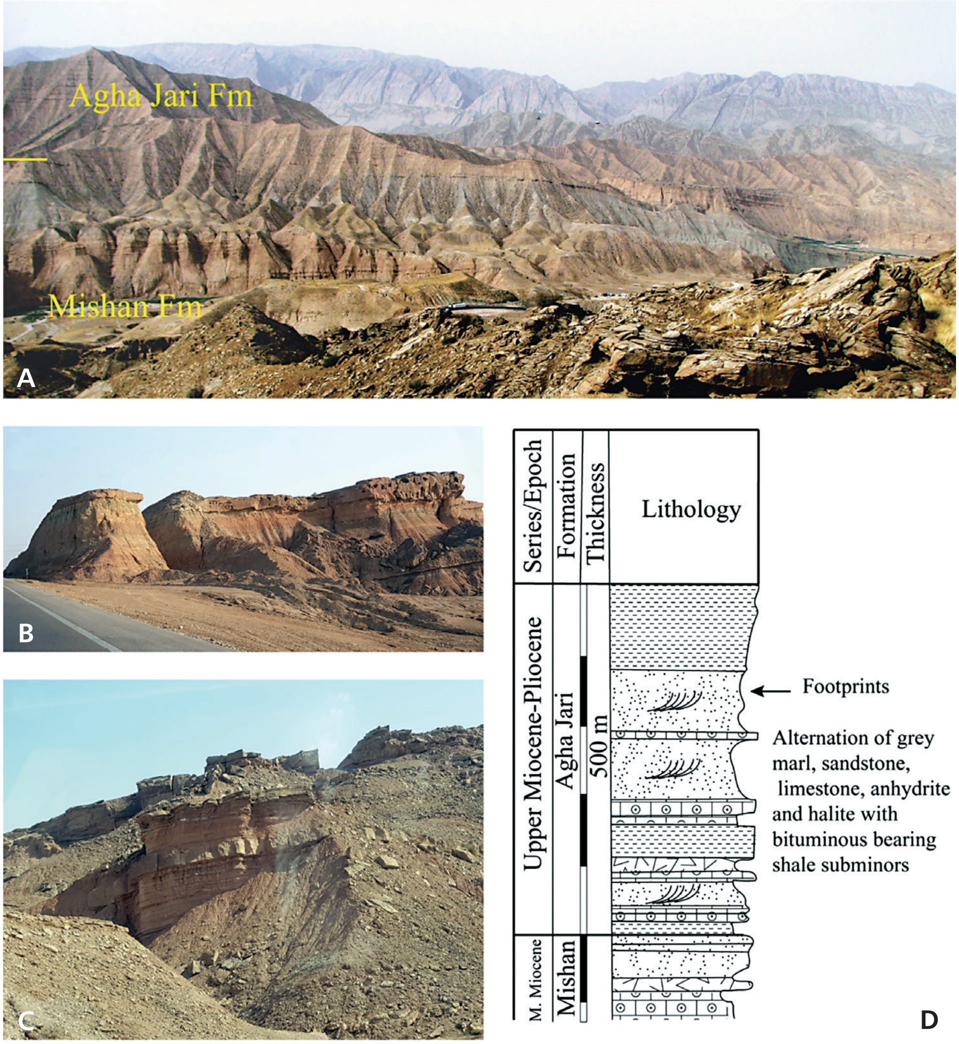

Figure 4. Agha Jari Formation outcrops and stratigraphic column in the Konar Takhteh area. • A – Mishan and Agha Jari formations boundary (view towards south). • B, C – alternations of sandstone and shales of the Agha Jari Formation, south Konar Takhteh. • D – simplified stratigraphic column of the Agha Jari Formation in the south Konar Takhteh (A and D modified from Yazdi *et al.* 2013, with permission).

Systematic ichnology

Ichnofamily Koreanornipodidae Lockley *et al.*, 2006

Ichnogenus *Koreanaornis* Kim, 1969

***Koreanaornis hamanensis* Kim, 1969**
Figures 6, 8, 9

Material. – More than 50 collected footprints, imprinted in five sampled slabs.

Description: Small tetradactyl footprints were preserved as convex hyporelief in the lower bedding plane of fine- to medium-grained brown sandstone. These footprints include three slender digit imprints, isolated or joined at the heel. The middle digit (digit III) impression is larger than the lateral ones. The hallux impression (digit I) is smallest and is only known from specimens S3 and S4. Claw impressions are visible at the tips of digit impressions. Digit impressions are lanceolate. Digital pads are not commonly recognizable, but some footprints show three pads in the medial or lateral digits. Digit imprints are arranged asymmetrically in the footprints so that digit II is smaller than digit IV. Only three trackways were distinguished. Table 2 shows the measurements of these footprints.

Remarks. – The morphology and size of the studied footprints are very similar to *Koreanaornis hamanensis* from the Cretaceous Haman Formation of Korea (Kim 1969). *Koreanaornis hamanensis* is tetradactyl tracks, but generally the digit I impression may not be well preserved and such tracks are reported as tridactyl imprints (Lockley *et al.* 1992, 2006, 2012; Camens & Worthy 2019). The authors compared *K. hamanensis* to tri- to tetradactyl avian Cretaceous and Cenozoic footprints. Thus, *K. hamanensis* differs from *Goseongornipes markjonesi* Lockley *et al.*, 2006, by greater width, wide divarication angles between

Table 2. Measurements on *Koreanaornis hamanensis* in the studied samples (in millimeters).

TL no.	S	P	FL	FW	DL			Ang.	
					II	III	IV	II–III (α_1)	III–IV (α_2)
1	–	–	13.6	22.7	14	13.6	11.3	40	59
2	–	–	16	26	13.5	11.6	13	38	68
3			10.7	18.4	8	8	9	55	70
4			15.7	21	10	12	8	57	50
5			23.6	22.3	11.8	18.2	9.2	45	60
6			9	18	7	8	7	50	63
7			26.3	29	9.2	17.1	13.1	77	54
8			26	30	13	18	10	68	45
9			10	14	7	8	6	50	58
10			20	22	9	18	12	40	65
11			8	10	5	7	4	–	–
12			–	–	–	–	–	–	–
13			20	21	11	18	8	53	50
14	90	175	23	25	10	16	8	38	80
15			15	24	7	12	10	48	60
16	50	–	20	25	10	13	11	50	65
17			18	23	9	14	10	55	65
18			17	30	13	15	12	62	65
19			13	27	17	12	10	53	65
20			15	21	6	12	11	52	60
21			20	30	13	17	12	80	55
22			19.1	30.8	15	11	14	65	75
23			14.1	23.3	12	19	13	40	45
24			17	22	12	12.5	12	29	52
25			23	35	16.6	17	19	25	115
26			46	46	33	31	17	40	88
27			28	32	12	21	12	50	73
28			11	28	10	13	14	85	45
29			28	29	8	21	17	75	40
30			19	19	8	13	14	75	70
31	69	127	20.8	27.5	10	17.5	19	53	53
33			23	21	12	16	11	80	32
34	54	–	18	22.5	7.5	13	14	65	50
35			22	24	13	14	13	65	35
40–44	102	214							
mean			20.45	26.6	12	15.8	12.7	56.2	60.8

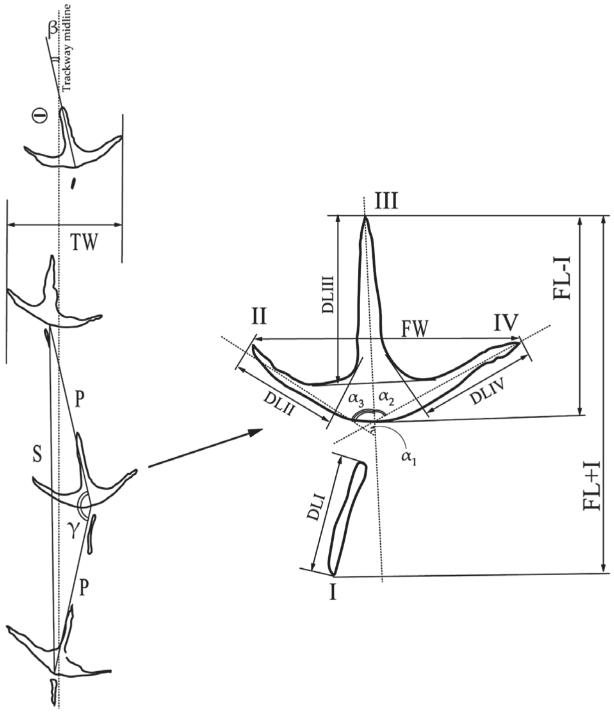

Figure 5. Method of measurement of geometry of bird footprints. Legend: S – stride length; P – pace length; TW – trackway width; I, II, III, and IV – digit numbers; DLI-IV – digit length; FL + I and FL − I – footprint length plus and without digit I, respectively; FW – footprint width; α1–3 – interdigital angle between digits II–III, III–IV and II–IV, respectively; β – angle of footprint rotation as negative (−) or inward to midline of trackway; γ – pace angulation. The trackway (a) of the sample S1 (IFMI-575) used as geometry pattern (see S1 in Fig. 6).

digits II and IV, and hallux impressions (Kim *et al.* 2013). Kordos (1985) however, established *Aviadactyla media* for small tridactyl bird footprints, and the main characteristics of this ichnospecies are the asymmetry of the footprint, and thin, stick-like, shallowly imprinted digit imprints. The studied footprints of *K. hamanensis* show higher digital angles between digit II and IV (112°) than in *A. media*.

The five ichnospecies introduced for *Koreanaornis* are *K. hamanensis* Kim, 1969, *K. lii* Xing *et al*., 2016, *K. sinensis* Lockley *et al*., 2008, *K. dodsoni* Xing *et al*. 2011 and *K. anhuiensis* Xing *et al*., 2018. Small size, wide, sub-symmetric, functionally tridactyl tracks with slender digit impressions and wide divarication angles between digits II and IV are the main characteristics of these ichnospecies. *Koreanaornis hamanensis*, *K. dodsoni* and *K. lii* have digit traces that do not join proximally on most tracks, but digit traces of *K. anhuiensis* connect proximally to a metatarsophalangeal pad (Xing *et al.* 2018). *Koreanaornis dodsoni* differs from *K. hamanensis* tracks in having smaller divarication angles between digits II and IV, greater overall track length and width, persistent absence of digit I, and absence of digital pad impressions

(Xing *et al.* 2011). *K. lii* is distinguished by a proximal footprint margin that is obtuse to nearly perpendicular to the digit III trace, high digit II–IV divarication, and a small digit I impression with a digit divarication I–II between 134°–160° (Xing *et al.* 2016). Tracks named *Aquatilavipes sinensis* Zhen *et al.*, 1995 from Sichuan Province, China, are probably a junior synonym of *Koreanaornis hamanensis*, but Anfinson *et al.* (2009) reclassified *A. sinensis* under the new combination *K. sinensis* Lockley *et al.*, 2008. The holotype of *K. sinensis* is 3.1 cm and 3.8 in length and width, respectively, with digit divarication of 115° (Zhen *et al.* 1995).

Ichnofamily Ignotornidae Lockley et *al.*, 2006

Ichnogenus *Persiavipes* nov.

Type species. – *Persiavipes gulfi* ichnosp. nov.

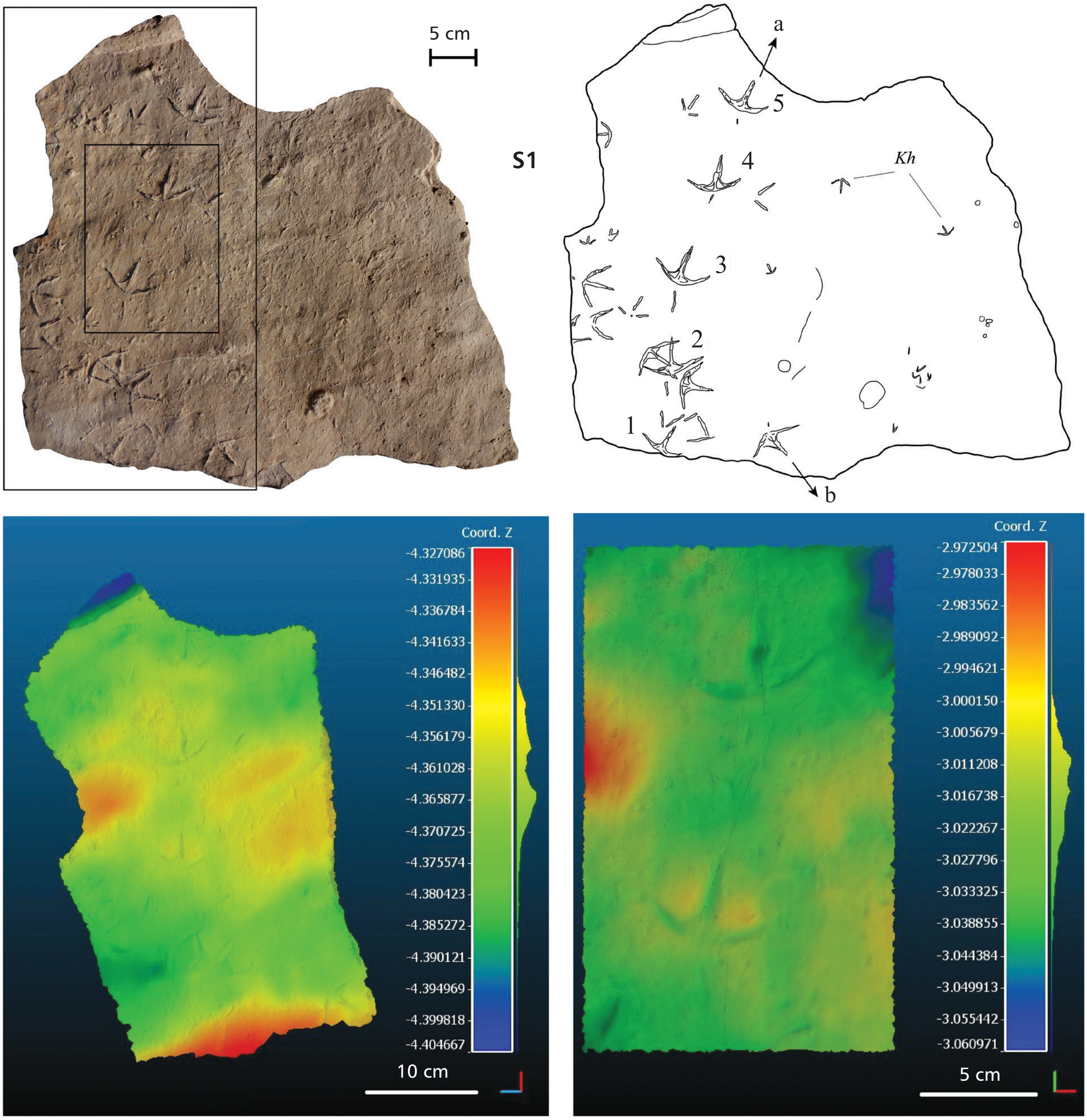

Figure 6. Photo, sketch and three-dimensional photogrammetric images of bird footprints in the studied slab of sample QGM-2888-S1 include *Koreanaornis hamanensis* (Kh), and holotype trackway of *Persiavipes gulfi* (trackway a), the quadrangles show position of photogrammetric images on the plaster molds. The perpendicular colour lines are X and Y coordinates and Z coordinates shows surface topographic variations.

Table 3. Measurements on *Persiavipes gulfi* in the studied samples S1 to S5 (in centimeters).

Sample No.	TW No.	Footprint No.	S	P	TW	FW	FL		DL				Interdigital angel		
							+I	−I	I	II	III	IV	II–III (α_1)	III–IV (α_2)	II–IV (α_3)
S1	a (Holotype)	1	20.1	9.95	5	4.7	–	3.3	--	2.3	2.3	2.7	61	72	136
		2				6.5	6.6	4.5	1.5	1.8	3.1	2.7	70	60	132
		3				5.7	6.7	4	2.25	1.4	2.7	2	52	57	109
		4				5.7	6.1	4.2	1.5	1.8	3.2	1.8	70	55	125
		5				5.7	5.9	4.3	1.1	2	3	2.3	63	62	125
	b	1	15.5	8.7	5.5	–	–	–	–	–	–	–	45	–	–
		2				12.7	10.5	7.5	–	3.7	3.7	3.7	75	50	123
		3				12.4	11.6	8.2	–	3.7	5.2	3.5	47	75	120
		4				14.2	12.7	8.2	1.0	4.1	3	3.7	70	62	130
S2	a	1	20.3	11.2	7	5.4	4.4	3	–	1.9	2.1	1.5	75	62	138
		2				5.8	5.9	3.5	1.5	1.9	2.7	1.9	48	80	130
		3				5.1	6.1	3.5	1.7	1.9	2.3	1.9	68	57	125
		4				3.8	5.4	3.6	1.5	1.5	2.3	1.9	45	55	82
S3	a	1	22	10.8	6.6	5.8	6	3.7	1.8	1.8	2.8	2.3	60	57	117
		2				6.5	5.5	3.5	1.6	2	2.5	1.8	60	75	135
		3				6.3	6.5	4	1.5	2.3	2	1.3	67	50	120
		4				6	7	4	–	2	2.3	1.5	65	67	130
	b	1	–	4	–	6.3	7	3.5	–	1.5	2.5	1.8	47	81	125
		2				5.3	6.3	4.2	1.5	2	2.7	2.3	65	54	117
	c	1	–	–	–	2.5	4	2.3	1.2	0.7	1.2	0.7	57	63	120
	d	1	–	8	–	–	–	2	–	0.7	1.2	–	55	–	–
		2				2.4	3	2	0.7	0.7	1	0.7	33	58	92
S4	a	1	19	9.4	5.1	5.3	6.6	4.2	2.0	1.6	2.6	2.6	62	55	118
		2				5.3	7.5	4.2	2.5	1.6	2.6	1.4	50	63	113
		3				4.7	6.3	4.2	2.2	1.9	2.5	1.3	63	47	112
	b	1	15	7.8	6.1	5.7	5.5	3.7	–	1.6	2.2	1.6	77	60	140
		2				5.5	6	4.4	1.8	1.6	2.3	1.7	53	60	114
		3				6	8.1	5	1.5	2.1	3.4	2.5	70	50	122
		4				5.8	7.4	5.3	–	2.3	3.4	2.1	60	54	104
		5				6.3	6	3.9	1.5	1.7	2.2	2.2	60	50	102
		6				6.1	5.3	3.7	1.5	2.1	2.2	1.9	65	60	125
		7				6.5	5.3	3.9	–	2.1	2.5	2.1	60	65	126
S5	a	1	9.5	5.6	6	5.3	–	3	–	1.7	2.6	1.8	45	70	115
		2				4.4	–	4.7	–	1.5	2.7	1.7	48	48	85
		3				6	–	3.2	–	3.2	2.2	2.2	50	52	104
		4				5	4.8	3.7	–	2.2	2.3	1.8	55	52	107
	b	1	–	–		4.8	6.8	3.4	1.6	1.8	2	2.2	40	50	90
	mean		17.3	8.2		6.04	6.5	4.09	1.58	1.96	2.54	2.03	58.2	59.8	117.3

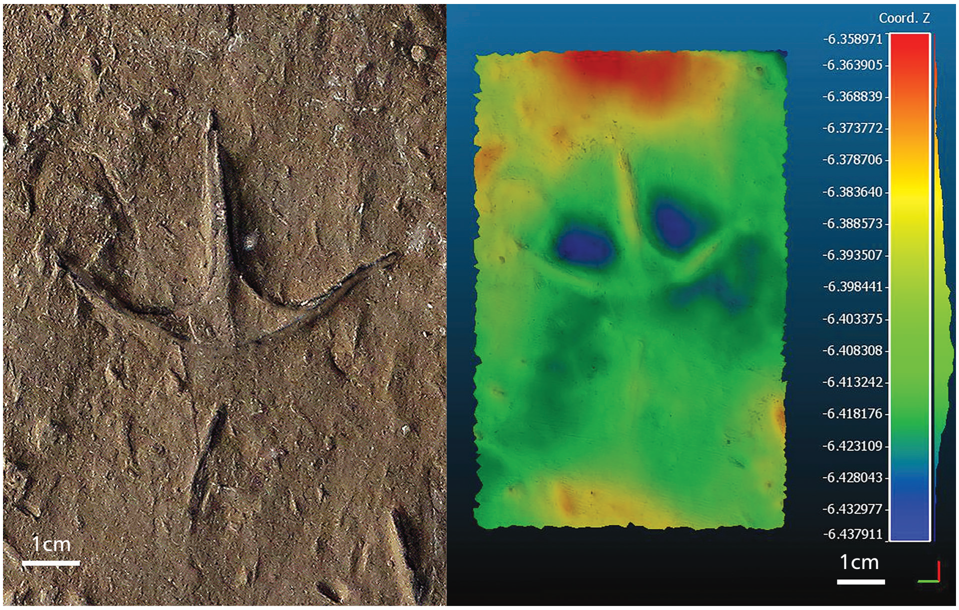

Figure 7. Well preserved footprint in the holotype trackway of *Persiavipes gulfi*, the third footprint of a trackway (a) of sample QGM-2888-S1, scale bar equals 1 cm. The perpendicular colour lines are X and Y coordinates and Z coordinates shows surface topographic variations.

Etymology. – *Persi* from Persia, the ancient name of Iran; *avi* from Greek Avia, and *pes*, Greek, pod.

Diagnosis.– Tetradactyl bird footprints, medium in size, composed of three slender, acuminate digit imprints,with claw marks. Digits connect to each other proximally with a semipalmate webbing. Digit III is longer than the lateral digits (II, IV), and the interdigital angle between II–III is smaller than the III–IV angle. A thin and delicate digit I imprint is long and oblique to the midline of the footprint. Digit I imprint does not touch the other digit imprints. Footprints slightly inward rotated.

***Persiavipes gulfi* ichnosp. nov.**
Figures 6–8

Material. – Twenty-five complete footprints arranged in seven trackways in five samples [sample QGM-2888-S1 (IFMI-575, plaster mold) and sample QGM-2888-S4 (IFMI-576, plaster mold) and samples QGM-2888-S3 to S5]. Holotype: Footprints of the trackway (a) in QGM-2888-S1 (S1 in Fig. 6, Fig. 7).

Etymology. – Gulfi from the Persian Gulf, sampled materials were located around the Persian Gulf.

Diagnosis. – As for the ichnogenus.

Description. – The footprints include four slender and straight digit imprints. Lateral digits arranged approximately symmetrical around the middle digit. Averages of interdigital angles are 58.2° and 59.8° between II–III and III–IV, respectively. Digit III is longer than the lateral digit imprints. No digit pad imprints are visible. Digit I imprint is smallest, has a needle shape, and is more oblique than the mid-line of footprints and separate from the forward-directed digit imprints. Interdigital web imprints cover about a quarter of digit length. The swollen rim of the interdigital web is retroflexed. Footprints are rounded proximally with slight relief. Table 3 shows the measurements on the studied trackways of *Persiavipes gulfi*.

Remarks. – The oldest bird or bird-like footprints have been reported from the Middle Jurassic (Lockley *et al.* 1992, Belvedere *et al.* 2011). Webbed bird footprints include *Gyeongsangornipes lockleyi* Kim *et al*., 2013 and *Ignotornis gajinensis* Kim *et al*., 2012 from the Early Cretaceous of South Korea. There are numerous reports of webbed bird footprints around the world, among them, there are 14 named ichnogenera that have been established for this kind of bird footprints (Tab. 4). The origin of webbed feet is related to the feeding habits and lifestyle of basal ornithuromorphs, which appeared in the waders and aquatic ornithuromorphs. Webbed footprints exclusively belong to birds or bird-like ornithuromorphs, and no webbed footprints have been reported for non-avian theropod dinosaurs. Although there are "webbed" toes on the dinosaur footprint *Irenesauripus mclearni* from the Lower Cretaceous of British Columbia (Harrington *et al.* 2005), this may be due to the substrate consistency, and it is not a truly webbed footprint. Three webbed toe imprints may be described as fully-webbed, such as *Anatipeda anas* Panin & Avram, 1962, *Anatipeda californica* Sarjeant & Reynolds, 2001, or on a part of middle digit (III) and fully on lateral toes, such as in *Leptoptilostipus pyrenaicus* Payros *et al*., 2000, *Presbyorniformipes feduccii* Yang *et al*., 1995, *Dongyangornipes sinensis* Azuma *et al*.,

Table 4. List of webbed bird ichnotaxa with their geometries (in centimeters).

	Ichnogenus	ichnospecies	FL	FW	Digit angle			age	Locality	Reference
					II–III	III–IV	II–IV			
1	*Anatipeda*	*californica*	8.4	7.0	42	42	84	Miocene	California	Sarjeant & Reynolds (2001)
		alfi	7.6	6.6	48	50	98	Miocene	California	Sarjeant & Reynolds (2001)
		recurairostrioide	~2.5					Miocene	Romania	Panin & Avram (1962)
		anas			30	55	85	Miocene	Romania	Panin & Avram (1962)
2	*Aquatilavipes*	*wallacei*	2.7 2.1–3.1	1.9 1.6–2.3	45–70	54–88	120–150	Oligocene	Sumatra	Zonneveld *et al.* (2012)
3	*Culcitapeda*	*ascia*	10.5	11.5	65	88	153	Miocene	California	Sarjeant & Reynolds (2001)
		tridens	6.1	8.2	47			Miocene	California	Sarjeant & Reynolds (2001)
		eccentrica	7.2	8.8				Miocene	California	Sarjeant & Reynolds (2001)
4	*Dongyangornipes*	*sinensis*	36.4	39.6	43.5	44	89	L. Cretaceous	China	Azuma *et al.* (2013)
5	*Goseongornipes*	*markjonesi*	4.1–4.5 (+ hallux)	4.2–4.5	70	70	140–150	Cretaceous	S. Korea	Lockley *et al.* (2006)
6	*Gyeongsangornipes*	*lockleyi*	3.08 (3.1–3.2)	4.00 (4.0–4.1)	69–71	56–58	125–130	E. Cretaceous	S. Korea	Kim *et al.* (2013)
7	*Hwangsanipes*	*choughi*	4.86 (4.80–5.00) (− hallux)	6.26 (6.08–6.60)			112.3	L. Cretaceous	S. Korea	Yang *et al.* (1995)
		*mcconnell*i	4 5.1	4.88			116	L. Cretaceous	Dakota	Mehl (1931)
8	*Ignotorni*s	*yangi*	4.3–6.3 (+ hallux) 3.3(2.8–3.7) (− hallux)	4.5 3.8–5.1	64	59	123	L. Cretaceous	S. Korea	Kim *et al.* (2006)
		gajinensis	6.75 mm	5.54	70	80	130	E. Cretaceous	S. Korea	Kim *et al.* (2012)
9	*Leptoptilostipus*	*pyrenaicus*	9.4 8–11.5	9.4 9–11.5			120	l. Eocene	Spain	Payros *et al.* (2000)
10	*Ludicharadripodiscus*	*edax*	4.2 (+ hallux)		60	55	115	l. Eocene	France	Ellenberger (1980)
11	*Phoenicopterichnum*	*rector*	10	15				Pleistocene	Argentina	Aramayo & Manera de Bianco (1987)
12	*Presbyorniformipes*	*feduccii*	9.2–9.5 (+ hallux) (6.2–6.4)	7.6–7.9 cm	50.8	49.3	100.7	Eocene	Utah	Yang *et al.* (1995)
14	*Roepichnus*	*grahami*	40–50	46–0			83–97	Miocene	Spain	Doyle *et al.* (2000)
13	*Sarjeantopodus*	*semipalmatus*	9.5 (+ hallux)	9.2	95	50	150	L. Cretaceous	Wyoming	Lockley *et al.* (2004)
14	*Uhangrichnus*	*chuni*	3.7 (3.3-4.62)	4.58 (3.8–5.4)	53.4	59.4	110–110.6	L. Cretaceous	S. Korea	Yang *et al.* (1995)
15	*Persiavipes*	*gulfi*	6.5 (3–12.7, + hallux), 4 (2–8.2, − hallux)	6.04 (2.4–14.2)	58.2	59.8	117.3	late Miocene–Paleocene	Iran	This paper

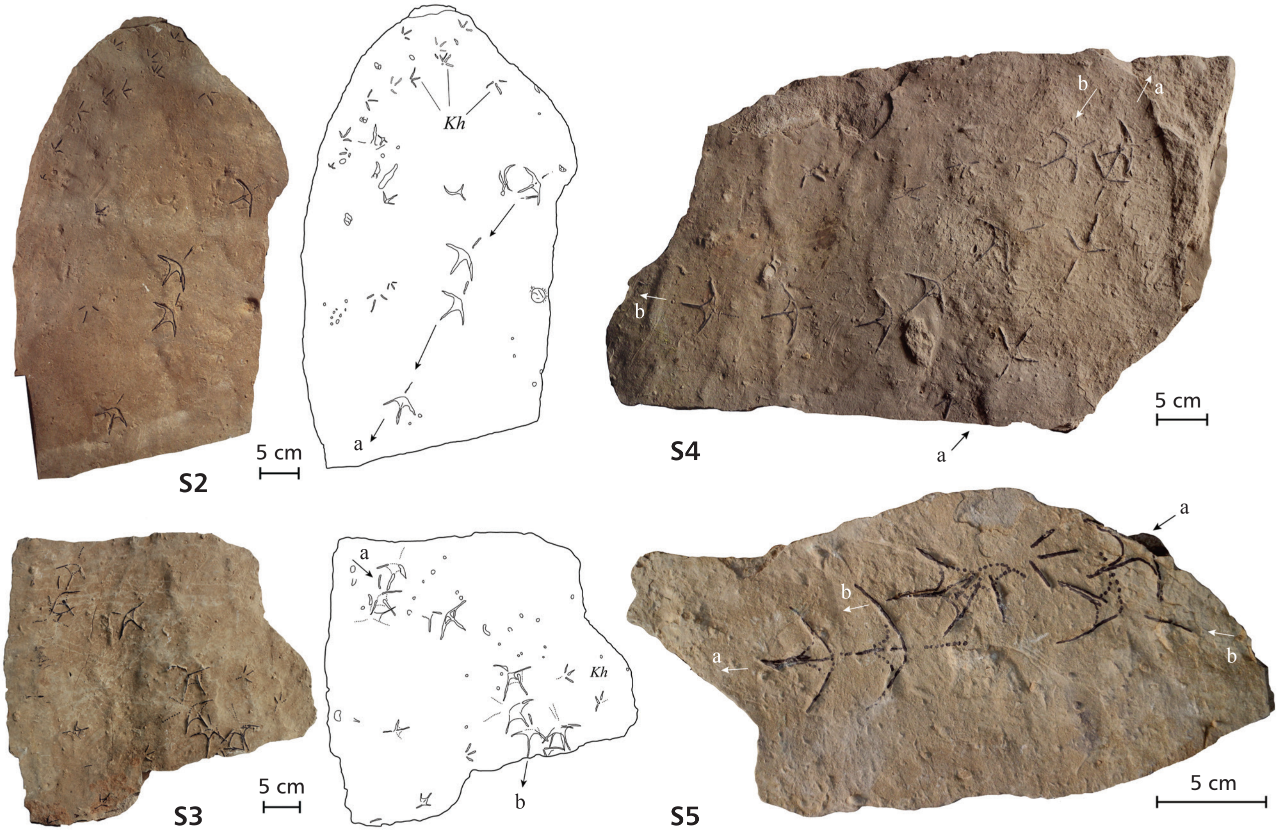

Figure 8. *Persiavipes gulfi* as semipalmate bird footprints and *Koreanaornis hamanensis* (Kh), in the samples QGM-2888-S2 to S5. Scale bars in cm.

2013 or asymmetrically only between the II–III or III–IV digit imprints, such as in *Sarjeantopodus semipalmatus* Lockley *et al*., 2004. *Persiavipes gulfi* is a tetradactyl semipalmate footprint, and the interdigital web involves the three forward-directed digits.

We classify *Persiavipes* under the ichnofamily Ignotornidae Lockley *et al*., 2006, together with the ichnogenera *Ignotornis*, *Hwangsanipes*, *Goseongornipes* and *Uhangrichnus* Yang *et al*., 1995. The ichnofamily Ignotornidae includes tetradactyl slightly assymetrical tracks with posteriorly directed hallux impressions typically showing significant medial rotation towards the trackway midline (Lockley *et al.* 1992). The diagnosis of the ichnofamily Ignotornidae was emended by Kim *et al.* (2012), and they considered it as tetradactyl bird tracks showing prominent, postero-medially directed hallux impressions comprising about one-third of total track length. The hypex between digits III and IV is more anteriorly situated than the hypex between digits II and III, with the tendency for development of an asymmetrical, semipalmate web that is more strongly developed between digits III and IV. Digit divarication between II and IV averages at least 110–120° (Tab. 5). Digit pad impressions are variable but sometimes show a 2–3–4 phalangeal formula corresponding to digits II, III, and IV. Step is typically short with a strong tendency towards inward rotation.

The ichnofamily Gruipedidae is known as tetradactyl avian footprints showing an axis either coinciding with, or at an angle to, that of digit III. Claws may be distinguishable, but the digits give no indication of digital pads or interpad spaces: the metatarsal pad is most often not impressed. Digits united or separated proximally. Webbing absent or limited to the most proximal part of the interdigital angle (Sarjeant & Reynolds 2001). At first, *Gruipeda* and *Alaripeda* were placed in Gruipedidae (Sarjeant & Reynolds 2001). In a later review, *Gruipeda*, *Ardeipeda*, *Antarchtichnus*, *Ignotornis* and *Tetraornithopedia* have been considered as ichnogenera of Gruipedidae (Lockley & Harris 2010). Among these ichnogenera, only *Ignotornis* is semipalmate, thus is belongs to Ignotornidae. Digit divarication in *Persiavipes* is the same as *Ignotornis* and smaller than *Goseongornipes*. Asymmetry of Ignotornidae is visible in the position of the hypex, so that the hypex between digits III and IV is more anteriorly situated than the hypex between digits II and III (Kim *et al.* 2006), which is visible more and less in *Persiavipes* (Figs 6–8). The range of FL + I of Ignotornidae is about 3.2–6.7 cm, and ratios of FL/FW and DLI/FL in the Ignotornidae equal to 0.67–1.37

Table 5. Geometry of the ichnogenera of the ichnofamily Ignotornidae (in centimeters) [data from Kim *et al*. (2012) (*); Mehl (1931), fig. 1 (**); Yang *et al*. (1995), fig. 5 (***); and Lockley *et al*. (2006), figs 9c and 20d (****)].

Ichnofamily	Ichnogenus	FL		FW	FL/FW	II^IV	DLI/FL	Footprint rotation (β)	Pace angle (γ)	web	Reference
		+ I	− I								
Ignotornidae	*Ignotornis*	~5.5*	~4*	4	1.37–1	105–125	0.33	−15	130**	Semipalmated Slightly III–IV > II–III	Mehl (1931)
	Hwangsanipes	6.68***	4.86	6.26	1.06–0.77	112.3	~0.28***	−10***	165	Full webbed	Yang *et al*. (1995)
	Goseongornipes	4.3	3.25	4.35	0.98–0.74	140–150	0.22–0.25	~−25****	170	Semipalmated	Lockley *et al.* (2006)
	Persiavipes	6.5	4.09	6.04	1.07–0.67	117.3	0.26	−15.2	165	Semipalmated	This paper

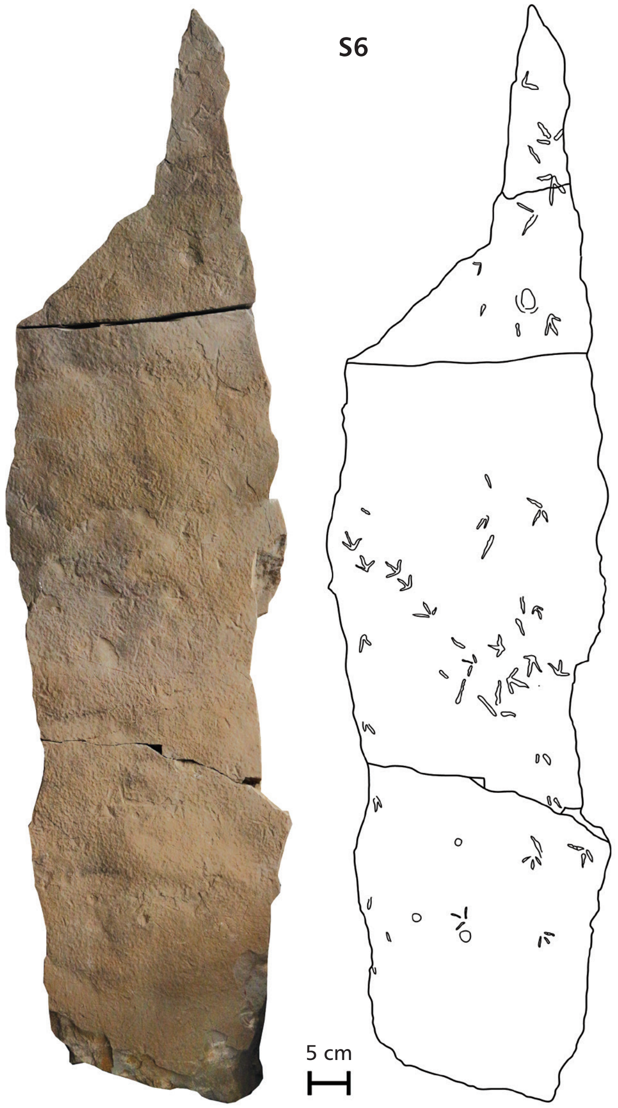

Figure 9. Poorly preserved *Koreanaornis hamanensis* as small sized bird footprints with slender digits (sample QGM-2888-S6).

and 0.22–0.33, respectively (Tab. 5). Although *Persiavipes* has the longest DLI (2.4 cm), its ratio of DLI/FL is equal to the mean of DLI/FL in the Ignotornidae. Ichnogenera of Ignotornidae have positive significant medial rotation towards the trackway midline. *Hwangsanipes* shows negative rotation (Tab. 5), and it may be the result of the arrangement of the footprints in a curved trackway (Yang *et al.* 1995, Fig. 5) or may be the result of measurement error by us on the figure 5 of Yang *et al.* (1995). The pace angulation is not constant in the ichnogenera and, of course, it is related to the speed of the bird.

In addition to morphological analysis of the ichnogenera of Ignotornidae, the morphology of *Persiavipes* is distinct from the other ichnogenera. Mehl (1931) mentioned a rudimentary web between digit I and II in the description of *Ignotornis mcconnelli*, this feature has been eliminated in the revised diagnosis by Kim *et al.* (2012). *Persiavipes gulfi*, however, shows a completely rounded posteriorly and isolated hallux imprint. *P. gulfi* differs from *Ludicharadripodiscus edax* Ellenberger, 1980 by the posteriorly rounded and well-developed digit I and high relief of the interdigital web. *Sarjeantopodus semipalmatus* (Lockley *et al.* 2004) is asymmetric semipalmate and has the interdigital web imprinted between digits III and IV.

Morphofamily Pecoripedidae Remeika *et al.*, 1995

Ichnogenus *Pecoripeda* Vialov, 1965

***Pecoripeda gazella* Vialov, 1965**
Figure 10

Material. – 16 footprints in the two large slabs (samples S7 and S8).

Description. – Hoofed footprints preserved as convex hyporelief (casts). Footprints have two imprints of hooves of slightly different size, and are overall heart-like in

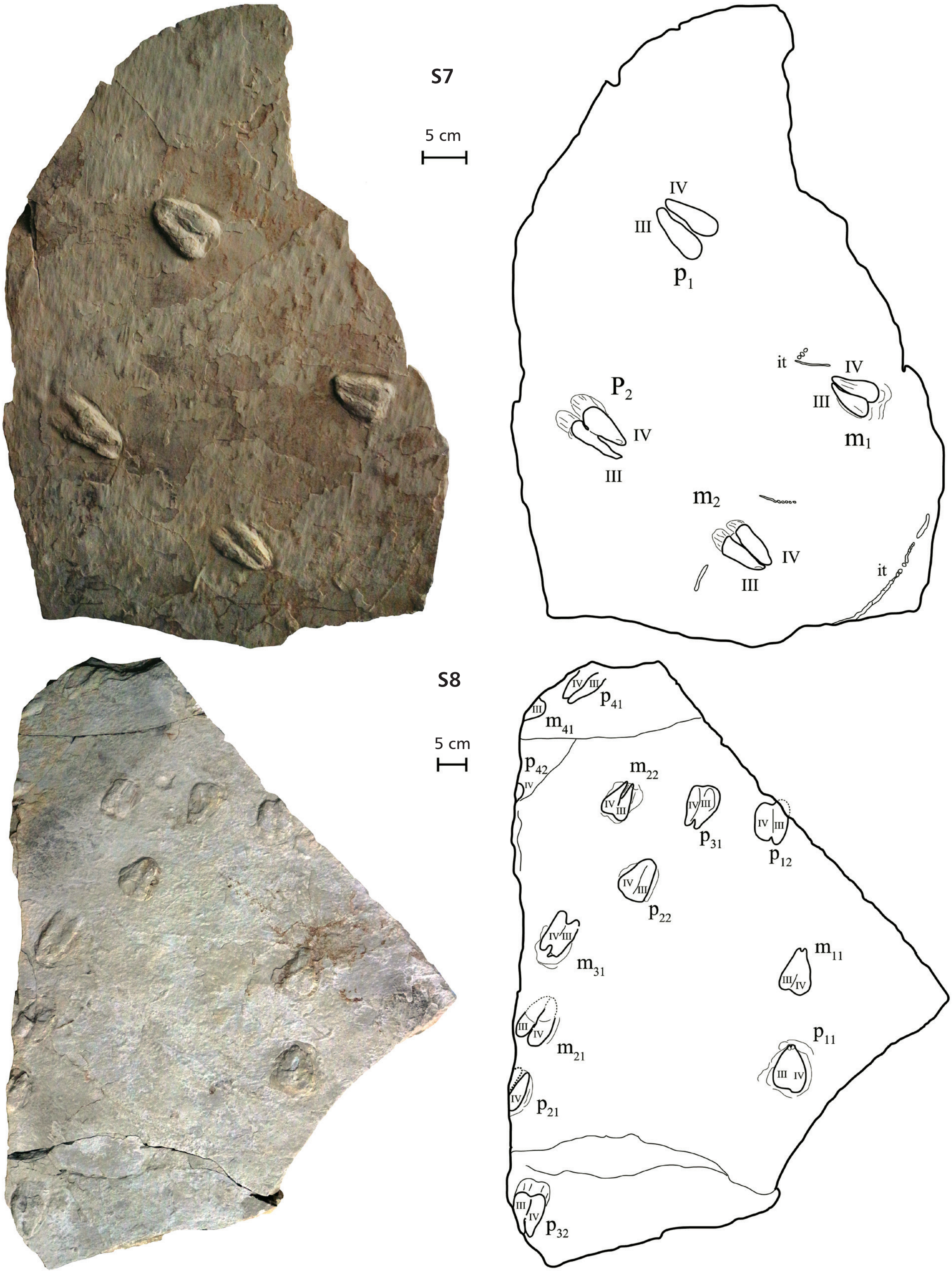

Figure 10. *Pecoripeda gazella* of studied slabs and coding of footprints. Abbreviations: p – pes; m – manus; it – invertebrate traces (samples QGM-2888-S7 and QGM-2888-S8).

Table 6. Measurements on *Pecoripeda gazella* of studied footprints of the Agha Jari Formation (in centimeters).

Sample	Trackway No.	Pes-Manus	FL	FW	FLIII	FWIII	FLIV	FWIV	$\frac{FL}{FW}$	$\frac{FLIII}{FWIII}$	$\frac{FLIV}{FWIV}$	Pace
1	1	p_1	6.4	5.0	6.2	2.4	6.2	2.4	1.28	2.66	2.66	–
		m_1	5.2	3.7	5.0	2.0	5.2	2.0	1.4	2.5	2.6	
	2	p_2	6.4	4.0	6.2	1.7	5.5	2.5	1.66	3.64	2.2	–
		m_2	5.4	4.0	5.0	2.0	5.0	1.8	1.35	2.5	2.77	
2	1	p_{11}	8.0	5.5	7.3	2.7	8.0	3.0	1.45	2.7	2.66	42.7
		m_{11}	8.0	5.3	7.5	2.5	8.0	3.0	1.50	3	2.66	
		p_{12}	8.0	5.5	8.0	2.5	6.5	3.0	1.45	3.2	2.16	
	2	p_{21}	–	–	–	–	–	2.5	–	–	–	40.5
		m_{21}	8.8	5.5	8.5	2.5	8.9	3.0	1.6	3.4	2.96	
		p_{22}	7.8	5.5	7.7	2.0	7.7	3.5	1.41	3.85	2.2	
		m_{22}	6.7	5.0	6.7	2.0	6.5	2.5	1.34	3.35	2.6	
	3	p_{31}	8.0	5.3	7.8	3.3	7.0	2.0	1.50	2.36	3.5	75.0
		m_{31}	8.0	4.5	8.0	2.3	7.5	2.3	1.77	3.47	3.26	
		p_{32}	7.5	5.5	7.0	3.0	7.5	2.5	1.36	2.33	3.00	
	4	p_{41}	–	4.2	–	2.3	–	–	–	–	–	–
		m_{41}	–	–	–	2.3	–	–	–	–	–	
		p_{42}	–	–	–	–	–	–	–	–	–	
	mean		7.2	4.8	6.2	2.3	6.8	2.5	1.46	2.99	2.71	52.7

shape. Hooves contact each other posteriorly or along the interior margin of hooves. The tips of hooves are sharp or slightly rounded. Backward, a short slippage trace shows sliding of hooves, and sediment deformations are visible around the footprints. The average ratio of footprint length (FL) to footprint width (FW), FL/FW is 1.46, and the inner hoof (digit III) is shorter and thinner than the outer one (digit IV) (Tab. 6).

Remarks. – We follow the diagnosis of the ichnogenus *Pecoripeda* and ichnospecies *P. gazella* by Sarjeant & Langston (1994). Artiodactyl footprints comprise 15 valid ichnogenera (Sarjeant & Langston 1994, McDonald *et al.* 2007, Abbassi *et al.* 2016), which were attributed to Cameloidea (*Bijugopeda* Sarjeant & Reynolds, 1999; *Camelipeda* Vialov, 1984; *Dizygopodium* Sarjeant & Reynolds, 1999; *Gambapes* Sarjeant & Langston, 1994; *Lamaichnum* Aramayo & Manera de Bianco, 1987; *Megalamaichnum* Aramayo & Manera de Bianco, 1987; *Paracamelichnum* Pérez-Lorente *et al*., 2009); Cervoidea (*Bifidipes* Demathieu *et al*., 1984; *Cervipeda* Vialov, 1965; *Megapecoripeda* Kordos, 1985; *Pecoripeda* Vialov, 1965); Anoplotheriides (*Anoplotheriipus* Ellenberger, 1980; *Diplartiopus* Ellenberger, 1980), or Bovoides. These ichnogenera are classified in the morphofamily Pecoripedidae (Remeika *et al.* 1995). Numerous characters have been used in the ichnotaxonomic definition of artiodactyl footprints, and most of them have morphological bases. Sedimentological features of the substrate control the morphology of the footprints, but lack ichnotaxonomic value. For example, the variety of sediment-water content and cohesiveness of fine-grained sediments caused different morphology in the footprints.

Scrivner & Bottjer (1986) classified four different major preservational morphologies of artiodactyl footprints in the Copper Canyon Formation (Eocene), California. These categories range from wet sediments with an ovate, deep depression described as a "squelch mark" to the distorted morphology of partially upward pulled footprints; and the best-preserved footprints that were impressed in a moist or "slightly damp" substrate and, finally, shallow impressions (usually less than 1 cm deep) with poor resolution of morphological detail. The composition of sediment (*e.g*., clays behave very differently than sands) and water content of sediments are main factors in preservational morphologies of the footprints. These categories are visible in an observation of the tracks of a herd of sheep walking on fine-grained clayey sediment (Fig. 11), so that very shallow and poorly registered footprints are preserved in sediment of low plasticity. It is assumed that the type of sediment does not change in the observed area (about 50 × 60 cm) and only the water content of sediments was changed (increased from the lower to upper part in Fig. 11).

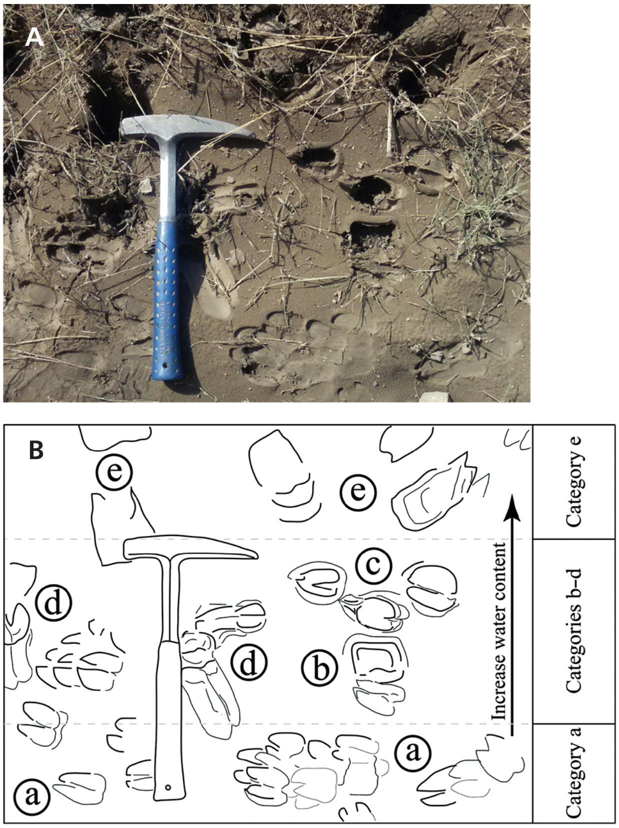

Figure 11. A variety of sheep foot imprints on fine-grained cohesive sediment with different water content (A) and sketched in five categories (B) (see text for details, photo by NA).

The potential of preservation of this kind of footprint is low, and the tips of toes are well preserved (Fig. 11Ba). An increase in the water content of sediments increases their plasticity, and the morphology of the footprints is distorted by the pastiness of the sediments. Hooves preserved as quadrangular, shallow depressions (Fig. 11Bb), deeply depressed footprints with strongly damaged rims around the footprints (Fig. 11Bc) and sliding imprints may occur (Fig. 11Bd). In the mostly wet sediments, footprints are impressed as very deep, oval-shaped traces (Fig. 11Be). Some of the named artiodactyl footprints are comparable to these kind preservations, for instance, *Bifidipes aeolis* Fornós *et al*., 2002, or *Paracamelichnum jumillensis* Pérez-Lorente *et al*., 2009, with a quadrangular shallow depression. Artiodactyl footprints of the Agha Jari Formation are well preserved with distinctive outlines; a few footprints show sliding imprints or slightly damaged rims of the footprints. These footprints are comparable to the mentioned categories c and d of *P. gazella* of the Agha Jari Formation, as they are large and elongate wedge shaped, and they differ from the *P. amalphaea* Vialov, 1965 (broad wedge-shaped and heart-shape outline), *P. satyri* (large, oval-triangular footprint), and *P. diaboli* (very wide and short tracks, with rounded to triangular outline).

Results and Discussion

Evaluation of the ichnodiversity is independent from the biodiversity, because ichnofossils are evidence for past behavior and may not reflect organismal diversity. Efficacy of environmental stress and stability, the ethological nature of trace-makers, taphonomy and stratinomy of trace fossils are main factors in the evaluation of ichnodiversity (Buatois & Mángano 2013). The three components of biodiversity in the community include niche, habitat, and province, which are known as alpha, beta and gamma levels in the biodiversity (Whittaker 1972). Ichnodiversity, however, is discussable in different aspects, so that some trace fossils are restricted to distinctive facies, and some others are known as facies-crossing.

Based on the reported occurrences of tetrapod trace fossils (Tab. 1 and Fig. 3), we focus on the evaluation of the vertebrate ichnodiversity of the Mio-Pliocene in the Persian Gulf region and adjacent areas (Central Iran) (Fig. 3), which is equivalent to the beta level of biodiversity. The Central Iran region shows greater ichnodiversity of Cenozoic vertebrate footprints, and this is most likely influenced by the larger number of ichnological studies carried out in this area (Fig. 3), so there is a sampling bias, due to a higher collecting effort. These reports include Eocene sediments, Birjand area, eastern part of the Central Iran (Ataabadi & Khazaee 2004), Oligocene sediments, Khaf area, northeastern part of the Central Iran (Abbassi *et al.* 2015), and late Miocene Upper Red Formation of the Eyvan-e key and Zanjan areas, northern and western parts of the Central Iran, respectively (Abbassi & Shakeri 2005, Abbassi & Amini 2008, Abbassi 2010, Alavi *et al.* 2016, Khoshyar *et al.* 2016). These reports show the ichnodiversity of the late Miocene Upper Red Formation is higher, which has a stratigraphic position equivalent to the Agha Jari Formation (and it is the equivalent stratigraphic unit in the Persian Gulf region, Fig. 3). The mammal tracks of the Upper Red Formation belong to carnivores, artiodactyls, and perissodactyls; bird footprints mostly are those of small to large shorebird tracks.

The Cenozoic terrestrial sediments of the Anatolian Plateau in the north Zagros Mountains may be other good candidates for vertebrate footprint discoveries. Oligocene artiodactyl and proboscidean tracks from the Sivas basin (Mesci *et al.* 2019) and Pleistocene human footprints from west Turkey (Ozansoy 1969) are terrestrial vertebrate footprints from the Anatolian Plateau.

The Mio-Pliocene track makers of the Persian Gulf region, however, are assignable to three classes, based on the track-makers and their size:

(1) Large-sized herbivorous mammals: this includes large mammal footprints from the late Miocene of the Baynunah Formation from Mleisa in the Abu Dhabi district, where

more than 14 trackways are attributable to Proboscidea by the round shape and large size of the footprints, with very large trackway stride lengths. These trackways present direct evidence that proboscidean social structure in the late Miocene comprised both herding and solitary behavioral modes (Bibi *et al.* 2012). Ichnotaxonomically, these footprints are identifiable as the ichnogenus *Proboscipeda* Panin & Avram, 1962. The Baynunah Formation contains very diverse vertebrate body fossils such as those of elephant, hippopotamus, horse, antelope, wolverine, hyaena, saber-tooth cat and primate (Hill & Whybrow 1999, Gilbert *et al.* 2014). The body fossils of proboscideans of the Baynuneh Formation determined as *Stegotetrabelodon* Tassy, 1999. *Omanitherium dhofarensis* is known as the oldest proboscidean body fossils from the Arabian Peninsula from the early Oligocene of the Ashawq Formation, south Sultanate of Oman (Seiffert *et al.* 2012), and the Mukdadiya Formation of NE of Iraq has yielded mastodon fossils (Thomas *et al.* 1981). The Baynunah Formation, however, yields only proboscidean trackways in the Persian Gulf region. There are no other reports of proboscidean ichnofossils from other parts of the Persian Gulf region. Proboscidean tracks known from Central Iran include those from the late Miocene Upper Red Formation in the Zanjan area (personal observation). Proboscidean body fossils from the late Miocene of the Maragheh Formation (northwest Central Iran) include *Choerolophodon pentelici* and *Deinotherium gigantissimum* Bernor, 1986. Before the early Miocene, the Tethyan Seaway was, to a large extent, a natural barrier to land mammal migration between Africa and Eurasia; proboscideans are among the most prominent African immigrants, which arrived in Eurasia about 19 Ma ago via the *Gomphotherium* landbridge (Harzhauser *et al.* 2007). The Eocene tracksite of the Tarom Mountains in the western Alborz Mountains, north Iran, however, exhibits the oldest record of proboscidean footprints, and this indicates that proboscideans had reached the northern shore of Tethys by late Eocene time (Abbassi *et al.* 2017).

(2) Medium to small sized herbivorous mammals: this group includes artiodactyl footprints from both sides of the Persian Gulf: the Konar Takhteh and Chamchamal tracksites from the northern and northwestern Persian Gulf and the Musandam Peninsula tracksite from Oman in the southeastern Persian Gulf. Footprints of the Agha Jari Formation of Konar Takhteh, described herein, reach up to 8 cm in length and are attributable to Cervidae (*Pecoripeda gazella*). Artiodactyl footprints of the Mukdadiya Formation of Chamchamal differ from the Agha Jari or Musandam footprints (Karim *et al.* 2003). The Chamchamal tracksite includes two kinds of artiodactyl footprints; larger footprints with divergent toe imprints with a 7 cm length are similar to *Bifidipes velox* Demathieu *et al.*, 1984, and smaller, heart-shaped footprints are 4–5cm in length. These small footprints resemble *Pecoripeda diaboli* Vialov, 1965. The Oman artiodactyl footprints were not determined ichnotaxonomically, because the original tracks have not been found. On the other hand, the large size of epireliefs of the footprints (well over 25 cm in length) are preserved in poorly consolidated aeolian deposits, and the original size of the footprints may have been much smaller than the underlayer containing the footprints. However, considering the artiodactyl characteristics of these footprints, they were assigned to the ichnological order Artiodactipedida (Vialov 1966, Schulp *et al.* 2011).

Late Miocene artiodactyl and perissodactyl skeletal fossils in the adjacent areas of the Persian Gulf are: *Hipparion*, Suinae, *Hippopotamus*, Giraffidae, and Bovidae from the Baynunah Formation (Brunet & Heintz 1983, Whybrow & Clements 1999), Giraffidae and Bovidae from the Agha Jari Formation of Mesopotamia of Iraq (Al-Zubaidi & Jan 2015), *Hipparion* from Mukdadiya (Thomas *et al.* 1981) and Suidae, Cervidae, Giraffidae, and Bovidae from the Maragheh Formation (Bernor 1986). Based on the sizes of the footprints, Suidae, Cervidae and Bovidae could be candidates as track-makers for artiodactyl footprints in the Persian Gulf region.

(3) Birds: bird footprints represent the first documents of vertebrate ichnites in the Persian Gulf region from the Lahbari Member of the Agha Jari Formation at Jabal Hamrin Mountain, western Iran (Lambrecht 1938, Abbassi *et al.* 2015). The Mio-Pliocene Agha Jari Formation of the Zagros Mountains and its equivalent Mukdadiya Formation in northeastern Iraq yield abundant large to small sized bird footprints. The large bird footprints of these formations at Jabal Hamrin Mountain on the Iran–Iraq boundary (Lambrecht 1938) and in the Chamchamal area in northeastern Iraq (Karim *et al.* 2003) include tridactyl imprints with backward-directed, large hallux imprints. These footprints are *Iranipeda abeli* and were made by willet birds such as Ciconiiformes (Doyle *et al.* 2000).

The bird tracks of the Agha Jari Formation of Konar Takhteh, however, consist of limicoline, small-webbed and un-webbed bird footprints, named *Koreanaornis hamanensis*, and *Persiavipes gulfi*. There are no reports of bird footprints from southern parts of the Persian Gulf. Bird body fossils of Struthionidae and Ardeidae, however, have been reported from the Baynunah Formation of Abu Dhabi and the Agha Jari Formation of Mesopotamia (Whybrow & Clements 1999).

The Miocene was a warm episode within the Neogene, contemporaneous with the closure of the Tethys seaway, which affected the paleobiogeography terrestrial biota. Mean annual temperature (MAT) of the early Miocene is estimated at about 16 °C. The Middle Miocene was the warmest period in the whole Miocene, and MAT increased to 17 °C to 19 °C. Climatic changes after the Miocene climatic optimum caused changes in plant assemblages and vegetation structure (Böhme 2003, Ivanov *et al.* 2007), which was important for herbivore distributions and caused the immigration of ecothermic vertebrates. Temperature and aridity of the late Miocene slightly decreased and displayed cycling in the warmer/cooler and humid/dryer conditions.

Climate changes during the Miocene–Pliocene interval, and the creation of new migration routes, are two main factors in the development of the new habitats and migration of vertebrates from the Arabian Peninsula to the Iranian plateau, and maybe *vice versa*. Ichnodiversity data of these regions, however, show increasing ichnodiversity from the interior of the Arabian Peninsula to Central Iran (Fig. 3). Based on current knowledge, it seems that the high ichnodiversity of Mio–Pliocene sediments of Central Iran (Upper Red Formation) relates to the high biodiversity of migrant track-makers after Mio–Pliocene tectonic and climate events, which created newly available habitat in Central Iran for immigrants from the Arabian Peninsula!? This hypothesis should be tested after the discovery of new tracksites in the Arabian Peninsula and the Persian Gulf region.

Conclusions

The Agha Jari Formation shows high potential for recording vertebrate footprints in the Zagros Mountains. Its mainly continental depositional environments created suitable substrates for the preservation of footprints. The Agha Jari Formation outcrops in the Konar Takhteh area, north Persian Gulf, record artiodactyl footprints assigned to *Pecoripeda gazella* and bird footprints assigned to *Koreanaornis hamanensis* and *Persiavipes gulfi*.

The Eocene Kashkan Formation, and the late Miocene–Pliocene Agha Jari, and Mukdadiya formations in the north of the Persian Gulf show higher ichnodiversity than the southern seaside of the Persian Gulf, so that only proboscideans and artiodactyl footprints have been previously reported from Cenozoic outcrops in these areas. The ichnodiversity of Cenozoic footprints in the Persian Gulf region increases from interior of parts of the Arabian Peninsula toward Central Iran. This suggests that the availability of new territories in Central Iran, after the closure of the Neotethys and the formation of the natural barrier of the Zagros Mountains, favored the increase of bio-and ichnodiveristy in the northern Persian Gulf.

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