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Recent vertebrate tracks in sandy substrates and their paleoenvironmental implications: examples from coastal Lithuania

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Abstract A diverse suite of vertebrate footprints documented along the coast of Lithuania offers insights into the distribution and preservation potential of tracks in sandy substrates. Whereas ichnotaxonomy is not conventionally applied to modern tracks, a case is made for using a footprint classification based on Vialov's (1966) nomenclature for both observed and predicted track distribution based on extramorphological characteristics of the tracemaker. Along a barrier spit (Curonian Spit) and mainland shoreline (Būtingė) sites, two general types of avian footprints (*Avipeda* isp), as well as three carnivore (*Bestiopeda*), four ungulate (*Pecoripeda, Suipeda, Hippipeda*), and two rodent (*Rodentipeda*) track morphotypes are described. The habitat preferences result in a predictable distribution of track assemblages with a potential of differentiating vertebrate ichnofacies (lagoon shoreline, open sea beach, dunes). The moisture content, possibility of freezing and rapid aeolian burial, and lithological anomalies (e.g., heavy-mineral concentrations) enhance the preservation potential of tracks. Once preserved, the context of trackways with respect to bedding surfaces determines their integrity and here a model of potential regional track distribution is proposed. Track formation and preservation in modern settings provides a useful guide to locating and studying vertebrate footprints and other traces in sand-dominated coastal and aeolian sequences.

***Keywords** • neoichnology • mammalian • avian • preservation • dune • Curonian Spit*

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INTRODUCTION

Vertebrate tracks have important paleobiological and paleoenvironmental implications, as summarized by Lockley (1986) and demonstrated in the increasing number of studies on fossil tracks in recent decades. As discussed in a classic ichnology work by Vialov (1966), detailed investigation into the formation and preservation of modern tracks (neoichnology) is essential for understanding the fossil traces of both vertebrate and invertebrate organisms. However, besides a few cursory studies and experiments in recent beach and dune environments (McKee 1947; Van der Lingen, Andrews 1969; Lewis, Titheridge 1978; Loope 1986; Lea 1996; Fornos *et al.* 2002) little research has focused on the distribution and preservation of modern mammalian and avian tracks in sandy substrates (Milàn, Bromley 2006). Several studies reported recent animal and human footprints from marine and lacustrine coastal deposits where most tracks are preserved on the upper surfaces of fine-grained sediments (Frey, Pemberton 1986; Cohen *et al.* 1991; Cohen *et al.* 1993; Huddart *et al.* 1999; Milàn *et al.* 2007b; Scott *et al.* 2009; Scott *et al.* 2010). In Cenozoic sand-dominated sequences, the tracks of ungulates and proboscideans have been largely studied in cross-section, though bedding-plane expressions (impressions or casts) also exist (Loope 1986; Lea 1996; Milàn *et al.* 2007b). Whereas laboratory experiments on track morphology and preservations are being increasingly undertaken, there is a need for neoichnological studies of modern vertebrate tracks in their natural environmental context (Laporte, Behrensmeyer 1980; Martin 2003; Milàn, Bromley 2006; Hasiotis *et al.* 2007; Genise *et al.* 2009; Platt *et al.* 2012; Platt, Hasiotis 2014). Holocene coastal environments (beaches, dunes, inlet channel margins) and their sedimentary sequences provide ready access to a variety of mammalian and avian traces and serve as modern analogues of numerous coastal formations in the rock record.

The Baltic Sea coast of Lithuania presents an ideal setting for neoichnological analysis of modern mammalian and avian tracks in sandy substrates due to a diverse animal community that ventures from forested areas (*palve*) onto bare beach and dune surfaces. The combination of this species diversity and a limited number of total animal species (35–40) in each order and family mean that in some cases a particular track may be attributed to only one species. In addition, the wide barrier spit, which was the focus of this study, has two shorelines (sea and lagoon), with some animal species confined to one side of this coastal landform.

The goals of the paper are to: 1) describe the morphology and distribution of mammalian and avian tracks and the most likely tracemakers in various subenvironments along the coast of Lithuania; 2) demonstrate the validity of the vertebrate track classification of Vialov (1966) in order to provoke the application of his ichnotaxonomy to recent traces, and 3) discuss the paleoenvironmental implications of the observed track distribution and preservation.

STUDY SITES

Two coastal sites in Lithuania were chosen for a field investigation of modern mammalian and avian tracks (Fig. 1). Most photographs in this paper were taken in early November 2008, but observation of tracks and tracemakers were also carried out in September–October 2005 and 2006. The main study region included several sites along the northern half of the Curonian Spit, a 1-3-km-wide and 100-km-long barrier spit, designated as a UNESCO World Heritage Site (Fig. 1). With prevailing westerly winds driving the aeolian transport, this landward (eastern) part of the spit is dominated by both active and stabilized Holocene dunes (Gudelis 1998; Bučas 2001; Buynevich *et al.* 2007; Gaigalas, Pazdur 2008). It has the highest coastal dunes in northern Europe (more than 60 m above sea level), which are part of the mid-late Holocene Great Dune Ridge (here called the "old dunes"). The sites where the tracks were documented include the Baltic Sea beaches of Nida ("sea beach"), the lagoon shoreline of Nida ("lagoon beach") and the adjacent Parnidis Dune (Nida site, Fig. 1B), as well as the forested dune field north of Preila (between Nida and Nagliu sites, Fig. 1B), where average monthly low temperatures remain below freezing from December to March. Much of the present foredune on the spit is part of an artificial protective dune belt. The second study region includes the mainland coastline of Būtingė (just south of the Latvian border; Fig. 1) and has a diverse assemblage of mammal tracks behind the main foredune. Several track types from this

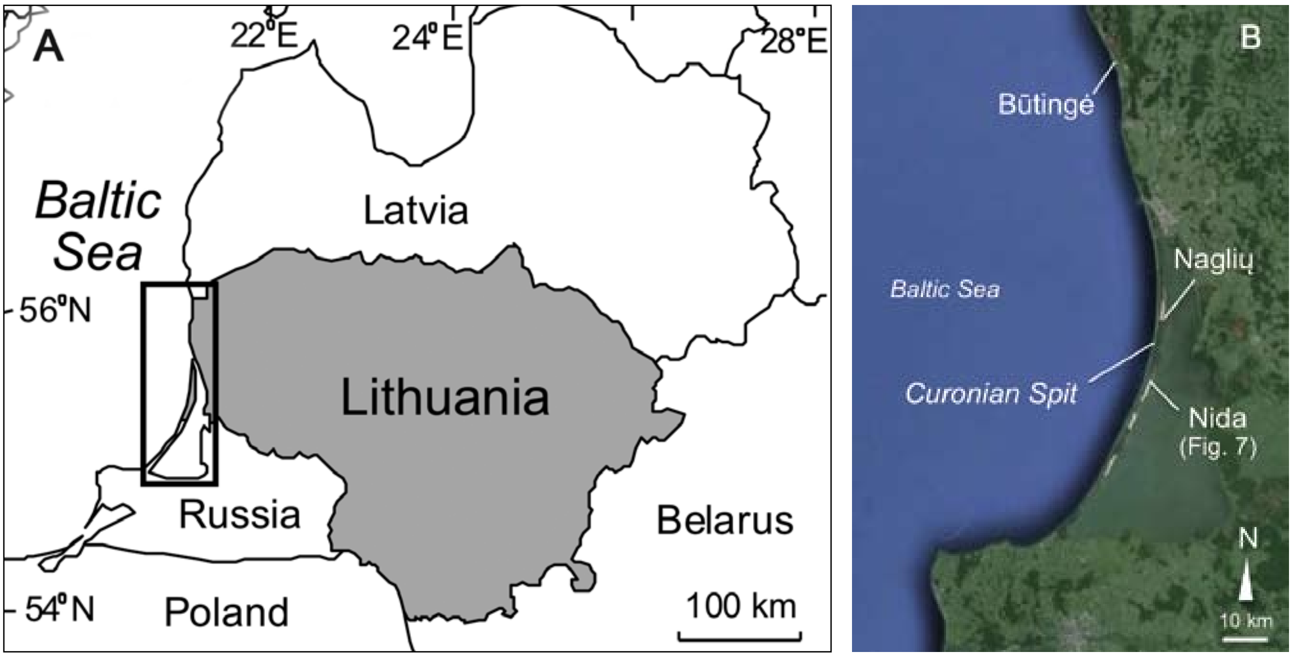

Fig. 1 Location of the study sites. A) Southeast Baltic Sea coast is a formerly glaciated area that today includes both mainland shoreline and extensive barrier spits backed by lagoons. B) Būtingė and Curonian Spit provide examples of these different physiographic coastal settings

assemblage are used to complement the recent footprints documented on the Curonian Spit. This study relies on field observations of live animals or tracks with different degrees of deterioration. Near surface geophysical investigations (200 MHz GSSI georadar) and several trenches and natural exposures are used to address the stratigraphic context of the traces.

TRACK CLASSIFICATION

Ichnotaxonomy of Cenozoic vertebrate traces is still undergoing revision and refinement (Lucas *et al.* 2007), often following the general systematics of Vialov (1965, 1966) or Sarjeant and Langston (1994). Although ichnogenetic or ichnospecific names are not conventionally applied to modern tracks, avian and mammalian tracks observed in this study have morphogenetic affinity to ichnotaxa proposed by Vialov (1966) (Table 1). This nomenclature was selected due to its descriptive morphological foundation (Vialov 1966; Scrivner, Bottjer 1986) and clear affinity with zoological systematics. This is particularly useful when dealing with recent or modern animal tracks (Murie 1974; Lockley, Peterson 2002; Martin 2003). Thus, considering a potential for preservation in the sedimentary record, a feline track can be safely attributed to *Felipeda* (feline) ichnosubgenus of *Bestiopeda* (carnivore) ichnogenus, as it will be recognized as such in its fossil equivalent. However, ichnospecies names assigned by Vialov (1966) to specific felid tracks in Cenozoic sequences of western Ukraine (e.g., *Bestiopeda bestia*, etc.), should not be applied to modern traces due to their narrow range of diagnostic morphological attributes (Lucas 2007). In this paper, Vialov's (1966) names and those that logically follow his terminology are therefore used for facility of reference.

For facility of reference, especially when using maps of track distribution, ichnogeneric notations are proposed such that major generic groups (Vialov 1966) are represented by capital letters, e.g. carnivore tracks *(Bestiopeda, B)*. The main groups of tracks are outlined below and include new track morphotype names derived from zoological sub-family names, since their modern tracemakers are known to species level. Where further subdivision is possible, it is followed by a lower-case letter commonly synonymous with a family, e.g., canine tracks *Bestiopeda* (*Canipeda*) (Vialov 1966) are designated as *Bc*, feline tracks as *Bf*, and so on.

Table 1 Tracemakers and environmental settings where their footprints were observed or expected. Also shown are ichnogeneric names (neutral genus in bold; after Vialov, 1966) that can be applied to a trace, if preserved in the sedimentary record

Tracemaker	Environment	Ichnotaxa
Birds		***Avipeda*** (***A***)
gull, duck (webbed)	sea and lagoon beaches	*Anatapeda* (*Aa*)
shorebird (non-webbed)	beaches, active dunes	*Charadriipeda* (*Ac*)
Carnivores		***Bestiopeda*** (***B***)
fox[1]	lagoon and sea beaches	*Canipeda* (*Bc*)
raccoon dog[2]		
domestic dog		
mink[1], weasel, otter, badger, marten, stoat	lagoon beach, foredunes	*Mustelipeda* (*Bm*)
seal[2]	sea beach	*Phocipeda* (*Bp*)
Ungulates (ruminating artiodactyls)		***Pecoripeda*** (***P***)
moose	old dunes, forest (palve)	large *Cervipeda Pc*(*a*)
deer	vegetated backdune	small *Cervipeda Pc*(*b*)
Ungulates (non-ruminating)		***Suipeda*** (***S***)
wild boar	lagoon beach, old dunes, forest (palve)	*Suipeda* (*Ss*)
Ungulates (perissodactyls)		***Hippipeda*** (***H***)
horse	sea beach and dunes (historical)	
Rodents		***Rodentipeda*** (***R***)
beaver	lagoon beach, sea beach[3]	*Castoripeda* (*Rc*)
muskrat[2]	lagoon beach	*Muroipeda* (*Rm*)

[1] Most likely tracemaker in the group based on track characteristics (see text for discussion).

[2] Tracks were not observed in the field; environment is based on habitat preferences.

[3] Recent reports.

Avian footprints have been described using both Vialov's (1966) and other classifications (Greben, Lockley 1993; Sarjeant, Langston 1994; Doyle *et al.* 2000; Mustoe 2002; De Valais, Melchor 2008; Genise *et al.* 2009). In the present study, the observed bird tracks (*Avipeda, A*) belong primarily to the gulls, ducks and other shorebirds and are subdivided into two broad groups: 1) tracks with curved outer toes (digits II and IV) most likely made by gulls (larids) or ducks *Avipeda* (*Anatapeda; Aa*) and 2) three- or four-toed (digits I [hallux], II, III, and IV) tracks with relatively straight toes, produced by other shorebirds and designated *Avipeda* (*Charadriipeda; Ac*). This nomenclature differs from that of Sarjeant and Langston (1994) and adopted by Mustoe (2002), who assign webbed tracks to *Charadriipeda*. In the study area, small coastal ducks and gulls leave nearly identical webbed tracks and individual tracks in a trackways that may lack the web print would still belong to *Aa* type based on overall morphology.

All carnivore tracks are grouped into ichnogenus *Bestiopeda* (*B*), which are further subdivided into subgenera/families, e.g., dog (*Canipeda, Bc*), cat (*Felipeda*, *Bf*), bear (*Ursipeda*, *Bu*), weasel family (*Mustelipeda, Bm*), seal and related pinniped (*Phocipeda, Bp*) tracks, and so on. The few bears and felines (lynx) that inhabit mainland Lithuania and are absent in the study area, therefore most observed carnivore tracks were of *Bc* and *Bm* types. For other groups, such as seals, their environmental distributions can be predicted based on the restriction of these animals to the beaches on the Baltic Sea side.

Ungulate footprints have been subdivided into those of artiodactyls (even toed) and perissodactyls (odd-toed), *Artiodactipedida* and *Perissodactipedida* of Vialov (1966). Artiodactyl footprints are subdivided into those by ruminating (*Pecoripeda, P*) and non-ruminating (*Suipeda, S*) animals. Both deer and elk (European moose) are representatives of the *Pecoripeda* (*Cervipeda*) group (*Pc*) and are distinguished further based on the tracemaker. *Suipeda* group (hippopotamus and pig) in this region includes the wild boar and is designated (*Ss*). The only perissodactyls are represented by domesticated horses, which probably left numerous tracks (*Hippipeda, H*) during the medieval occupation of the Curonian Spit. The modern horse (*Equus* spp.) would be responsible for this track type.

Traces produced by rodents include actual foot impressions (*Rodentipeda, R*), drag marks and gnaw marks on the trees. The tracks themselves are subdivided into those made by beavers (*Castoripeda, Rc*) and muskrats *Muroipeda* (*Rm*), and can be similarly extended to other representatives of rodents not observed in the present study. Again, it is important to note that the classification is designed for facility of reference and potential application to traces preserved in the sedimentary record, rather than erecting new ichnotaxonomy for modern traces (cf. Vallon, Kjeldahl-Vallon 2011).

TRACK TYPES AND TRACEMAKERS

Tracemaker identification was based on comparison of the diagnostic features of the tracks (Murie 1974) with modern bird and mammal species present in the region and several field observations of the trace-making activity. Most tracks were made on medium-to-coarse, beach and dune sands, with beach sands having slightly greater moisture content than aeolian sand. Detailed descriptions of track size and morphology are beyond the scope of this paper and the reader is referred to the photographs to evaluate each track (Figs 2–6). Below are the descriptions of key parts of each track type (trackway patterns, numbers of digits, claw impressions, etc.) and the most likely tracemakers.

Bird tracks – *Avipeda* (*A*)

As discussed above, the tracks found on the surface of the beach and coastal dunes are represented primarily by ducks (*Anatidae*), gulls, and other shorebirds (*Charadriformes*). In this study, *Avipeda* tracks were differentiated on the basis of the webbing being present (*Aa*) and footprints lacking the webbing (*Ac*), although preservational bias certainly affects this aspect (Falkingham *et al.* 2009; Falk *et al.* 2011; see discussion below).

Anatapeda (***Aa***) Several trackways showing the webbing between the toes occur along the Baltic Sea beach (Fig. 2A, B). Based on field observations and track morphology, they are attributed to several species of gulls (Larids). In moist beach sand, some trackways extend for several meters, often showing sharp or wide turns. Several species of small ducks present along the sea and lagoon coast would also produce webbed prints. Without direct observation and further studies, it may not be possible to distinguish the gull and small duck tracks on the beach. Although larids are different from the ducks, the *Anatapeda* morphotype is used here to denote all webbed traces.

Charadriipeda (***Ac***) All non-webbed, three- and four-toed (digits II, III, IV and hallux) avian tracks are attributed to various shorebirds and lacking web impression (Fig. 2, C–F). Most of these tracks occur along the lagoon shoreline and on Parnidis Dune. Some trackways have straight shallow grooves between footprints, which could be tail or beak drag marks (Fig. 2D, F). Due to observations being conducted in late fall, the *Ac* tracks were most likely produced by wintering four-toed birds that favor open sand areas of foredunes and old dunes (e.g., tawny pipit, *Anthus campestris*, which has a relatively long tail).

Carnivore tracks – *Bestiopeda* (*B*)

Canipeda (***Bc***) Carnivore racks are shown in Figs. 3, 4A, B and 5A. The tracks of the dog family include those of widespread red fox (*Vulpes vulpes*) and domestic dog. The fox is the most likely producer of the documented tracks due to their widespread occurrence and the lack of human tracks next to fresh canine footprints. Numerous four-toed canid (*Bc*) footprints with claw (ungual) impressions have been found behind the foredune ridge at Būtingė (Fig. 3A), one associated with a burrow (Fig. 3B). On the Curonian Spit, *Bc* tracks of various sizes run in both directions along the Curonian Lagoon shorelines at the base of Parnidis Dune (Fig. 3). Here, they occur in the same animal trail as the wild boar (*Ss*) trackways (Fig. 5A). Segments of *Bc* trackways were also observed near the crest of the Parnidis Dune (~20 m above lagoon level; Fig. 3D) and on the Baltic Sea beach and foredunes where they are frequently associated with bird tracks and show various degrees of preservation.

Mustelipeda (***Bm***) Several members of the weasel family occupy the two study sites: badger (*Meles meles*), pine marten (*Martes martes*), stoat (*Mustela erminea*), and weasel (*Mustela nivalis*), the endangered otter (*Lutra lutra*), and the American mink (*Lutreola vison*). The latter may be responsible for a clear five-claw impression found associated with canine tracks behind the foredune at Būtingė (Fig. 4A). Some five-toed prints lacking claw marks occur along the lagoon shoreline on the Curonian Spit and may also be attributed to a mustelid (Fig. 4B).

Phocipeda (***Bp***) Gray seal (*Halichoerus grypus*) is an endangered (Red List) species reported to be

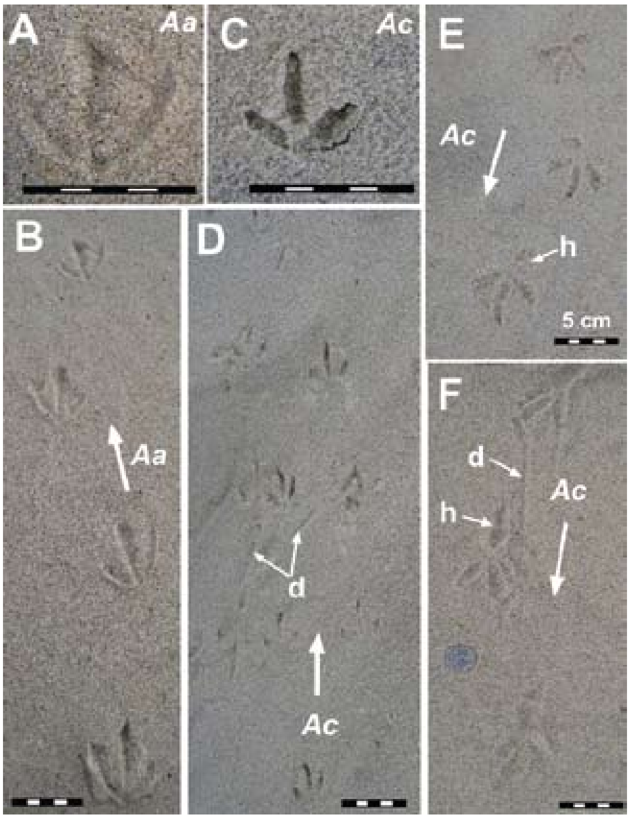

Fig. 2 Examples of *Avipeda:* A) A webbed track *Aa* left by a gull along the Baltic Sea beach, Nida, Curonian Spit (see text and Table 1 for track morphotype abbreviations). B) A trackway of *Aa* type, oriented parallel to the water line (to the left). C) Deep three-toed track *(Ac)* in moist sand on Parnidis Dune. Note the crack in cohesive sand. D) Numerous *Ac* tracks pointing uphill on the Parnidis Dune, with deep claw impressions and elongated (tail or beak?) drag marks (d). E) These four-toed *Ac* footprints with three digits and a hallux (h) were formed along a bedding plane on Parnidis Dune. F) Similar four-toed *Ac* footprints extend downslope on the lagoon beach with an elongated drag mark (d) between the top prints. On all photos, the scale bar is 5 cm long, with 1 cm increments

Fig. 3 Examples of *Bestiopeda* (*Canipeda*): A) Front and hind four-toed canid (red fox) tracks in a lightly vegetated area behind the foredune ridge at Butinge. The claw marks are clearly visible. B) A collapsed burrow with a clear *Bc* footprint to the right, Butinge. C) Several canid tracks oriented in opposite directions along the animal trail on lagoon shoreline in Nida, Curonian Spit. Note clear pad, toe, and claw impressions. The water line is to the left. D) Two *Bc* tracks oriented uphill on the Parnidis Dune. Note a section of cohesive sand collapsed under (downhill) of the track on the right. Similar structures are seen in some examples of uphill-oriented vertebrate tracks in the rock record (Lockley, 1986). These prints occur next to avian *Ac* tracks shown in Fig. 2D

confined to the Baltic Sea beaches. Although not observed by the author, the traces will be most likely represented by a body drag mark with flipper tracks on either side (Murie 1974).

Artiodactyl tracks – *Pecoripeda* (*P*) *and Suipeda* (*S*) Based on the original classification of Vialov (1966), all ungulate tracks are subdivided into those of even-toed (*Artiodactipedida*) and odd-toed (*Perissodactipedida*) animals. The latter can be subdivided further into suborders of ruminating (*Pecoripeda, P)* and non-ruminating (*Suipeda, S*) ungulates. Distinct representatives of these two groups are found in the study area.

As mentioned above, the only perissodactyl representative can be potentially preserved in the study area would include hoofprints of domesticated horses (*Hippipeda*; Vialov 1966).

Fig. 4 Examples of *Bestiopeda* (*Mustelipeda*) *and Pecoripeda:* A) A five-digit track exhibiting clear claw marks and a slight indentation of the pad. This track is most likely a mustelid (*Bm*) footprint found behind the foredune ridge at Butinge. B) The five-digit track (above) and overprinted tracks below may belong to a mustelid (*Bm*) or an aquatic rodent (muskrat, *Rm*) along the Curonian Lagoon beach at Nida. C) This large cervid track *Pc*(*a*) belongs to the elk (European moose) and was part of a long succession traversing the vegetated dunes north of Preila, Curonian Spit. Arrows point to well-pronounced dewclaw impressions. D) A small *Pc*(*a*) track was found in back-dune forested area of Butinge and most likely belongs to a small cervid, such as a roe deer. No dewclaw marks are present. Compare this track to the wild boar hoofprints in Fig. 5C, which are more rounded and are spaced close together

Pecoripeda (***Cervipeda***) (***Pc***) The elk or European moose (*Alces alces*) is the largest mammal in coastal Lithuania. In the old dunes north of Preila, a single 300-m-long trackway with large hoof size (10 cm) and dewclaw impressions (Fig. 4C) can be only attributed to this animal (Murie 1974). The large size of the tracks, as well as trackway width and stride, clearly distinguish the moose from its smaller neighbor, the roe deer (*Capreolus capreolus*). A possible track produced by a roe deer was photographed at Būtingė site (Fig. 4D). Both track types will fall in the *Pecoripeda* (*Cervipeda*) class and will require new species name for their classification similar to other *Pecoripeda* morphotypes described by Vialov (1966). Here, they are simply referred to as type (a) and (b) *Pc* tracks or Pc(a) and Pc(b) for moose and deer, respectively (Table 1; Fig. 4C, D), with a cautionary note that juvenile moose tracks may resemble large deer tracks. The latter may not be an issue in the sedimentary record, where most *Pc* tracks will represent similar environments.

Suipeda (***Ss***) The wild boar (*Sus scrofa*) is one of the most common re-introduced mammal species on

Fig. 5 Examples of *Suipeda:* A) Numerous wild boar (*Ss*) trackways extend along the Curonian Lagoon shoreline (water at left) in both directions. Many canid (*Bc*) tracks also occupy the same trail. The box outlines the area shown in Fig. 5B. B) A close-up of the lagoon beach trail shows the opposing tracks of both types *Bc* and *Ss*. Note clear dewclaw impressions on the boar track (small arrows). C) Several Ss tracks illustrating that dewclaw impressions seen in the lower track (arrows) may not always register (upper tracks). Compare to cervid track in Fig. 4D.

the spit (coincidentally, the animal species name has the same abbreviation as the suids family track name, *Ss*). In addition to trampled surfaces found in many forest openings, fields, and gardens, distinct boar prints (*Ss*) can be found in the spit interior (e.g., old dunes) and along the lagoon shoreline (Fig. 5). At the Parnidis Dune site, numerous *Ss* prints of nearly identical sizes run in both directions for hundreds of meters along the narrow damp strip of the lagoon shoreline (Fig. 5A). The tracks are comparable in size to roe deer footprints (Fig. 4D), but differ from them by having clear dewclaw impressions (Fig. 5B; 5C, bottom; Murie 1974). As discussed by Vialov (1966), in the absence of dewclaw marks (Fig. 5C, top), it may be difficult to distinguish the two families and a common ichnological order term *Artiodactipedida* should be used for all two-towed cloven-hoof ungulates. However, as seen in Figs 4D and 5C, the boar hoofprint is more rounded than cervid track and the toes are spaced close together (thinner interdigital ridge). The latter can also be a function of substrate consistency, with softer sediment causing more spread in the hooves (Vialov 1966; Scrivner, Bottjer 1986).

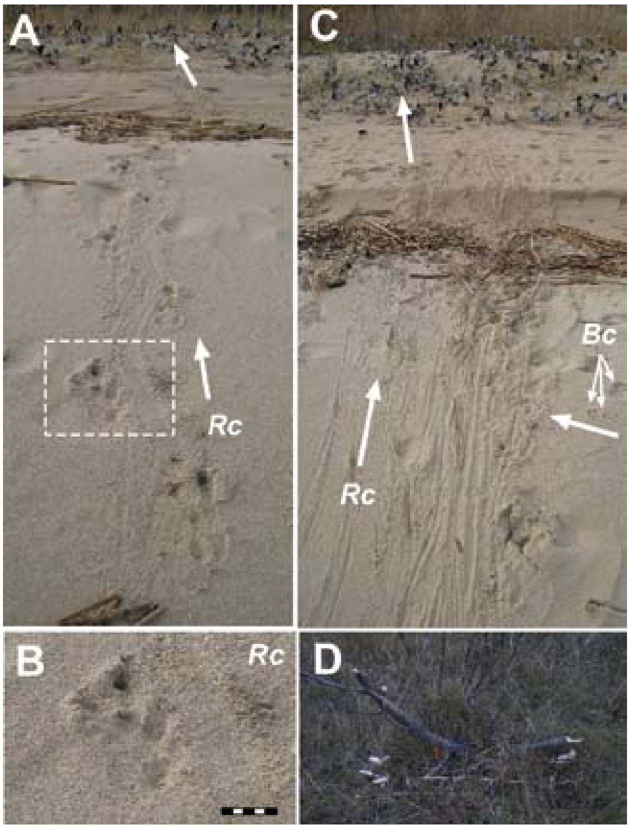

Fig. 6 Examples of *Rodentipeda:* A) This winding drag mark and alternating footprints most likely belong to a beaver and are of *Rc* type. The trail is oriented uphill, leading from the lagoon to the forested area. The box outlines the area shown in Fig. 6B; B) A close-up of the left footprint pair with a flat pad probably resulting from the webbed hind foot imprint; C) A wide nearly straight drag trail, possibly several superimposed trails, also attributed to *Rc*. Canid footprints (*Bc*) are oriented perpendicular to the trail. D) Gnawed branches of a small tree were found near the end of the beaver trail and serve as an independent trace of the animal's activity

Rodent tracks (*Rodentipeda*)

There are several species of large and small rodents present on the Curonian Spit, however only several distinct traces have been documented here and are attributed to large semi-aquatic species associated with the Curonian Lagoon.

Castoripeda (***Rc***) Beaver (*Castor fiber*) tracks consist of shore-normal drag marks of various width found at several locations along the Curonian Lagoon (Fig. 6A, B). These tracks overprint or are overprinted by those of carnivores (Fig. 6C) and wild boars. Farther landward, gnawed branches of small trees have been found associated with beaver paths (Fig. 6D). In recent years, there have been sightings of beavers along the Baltic Sea coast, both along the Lithuanian and Russian parts of the spit.

Muroipeda (***Rm***) Another coastal lagoon dweller, muskrats (*Ondatra zibethica*) have been introduced to the region and leave tracks similar to beavers (Murie 1974). Though no specific tracks have been observed during the study period, it is possible that some five-toed prints along the lagoon shore may be attributed to these rodents. Muskrats may also leave similar drag trails, but their hind prints lack the webbing and have smaller pace length (Murie 1974).

DISCUSSION

Track distribution and paleoenvironmental implications

Lockley (1986) summarized the role of dinosaur tracks as indicators of shoreline orientations, paleo-slopes, and substrate consistency. The tracks described in this study provide clear evidence for environmental and topographic control on animal behavior manifested by large trackway segments confined to specific sub-environments (Fig. 7). These trends, if preserved, can be used to infer paleo-shoreline trends. Extensive trackways of wild boar (*Ss*) and red fox (*Bc*) are present along the Curonian Lagoon shoreline, where they extend for several hundred meters and sometimes for kilometers. Due to the absence of tides, the trackways are confined to a relatively narrow swath just above the water line (cf. Scrivner, Bottjer 1986) and indicate an active preferred trail for an individual or a group of animals (Lockley 1986). It should be noted that game trails in any environment may be of considerable length and various degrees of substrate reworking intensity (Laporte, Behrensmeyer 1980) and thus other geological characteristics have to be considered before interpreting a coastal setting. Nevertheless, the association of diverse mammal and bird tracks, sometimes with invertebrate traces present, is a good indicator of paleo-shoreline environment.

In contrast, numerous tracks of mustelids (*Bm*), deer and moose (*Pc*), some birds, and any other animals that traverse major topographic or geological boundaries have low value as paleo-shoreline indicators (Fig. 7A). As discussed below, this pattern of activity also eliminates the possibility of the resulting tracks being preserved in a single bedding-plane exposure. Nevertheless, formerly large populations of moose, deer, as well as the use of domesticated horses for travel along the spit in historical times would suggest that, if preserved, *Pecoripeda* (*Cervipeda*) and *Hippipeda* (*Equipeda; He*) tracks, along with human footprints, are potentially numerous in sandy deposits of the Curonian Spit (Fig. 7B). Recent horse tracks have been reported from coastal sands of New Zealand (Van der Lingen, Andrews 1969; Lewis, Titheridge 1978) and are likely to occur in other coastal settings where domesticated or feral horses are found (Shackleford Island, North Carolina; Assateague Island, Virginia; Sable Island, Canada, and others).

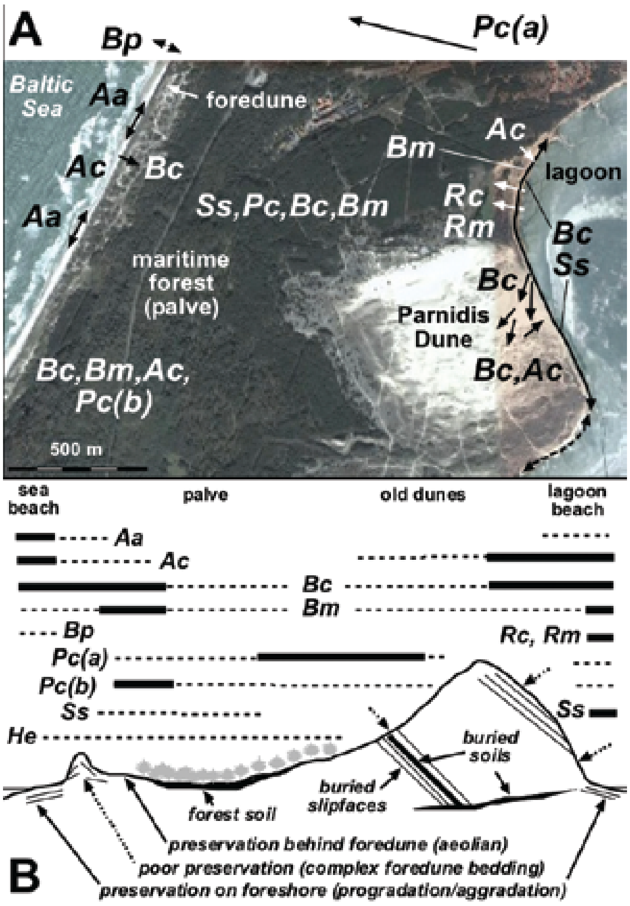

Fig. 7 A) Distribution of mammal traces on the Curonian Spit (September 2007 base photo from GoogleEarth). Some track types behind the foredune (*Bm,* small *Rc*) were plotted based on their occurrence in Butinge. The moose tracks (*Pc*(*a*)) found several kilometers north of Nida and the predicted range of seal tracks (*Bp*) are plotted above the photograph. Arrows denote trackway orientation. B) Summary diagram of track distribution (solid line segment – observed tracks) and preservation potential in modern environments and in the stratigraphic record. Dashed arrows indicate poor preservation potential. See text for discussion

Modern tracks can even be used to distinguish between lagoon and sea (or ocean) shorelines (Fig. 7A). For example, due to the habitat preferences of beavers and muskrats, tracks of these rodents (*Rc, Rm*) are found on the lagoon side of the Curonian spit. On the other hand, seal tracks (*Bp*), though not observed here, will be confined to the open sea beaches. Several species of gulls also prefer sea beaches to the lagoon shoreline, reflected in greater abundance of their webbed tracks (*Aa*) in the former. Further neoichnological studies and comparisons to the rock record, such as the recent work by Genise *et al.* (2009) on avian trackways in Argentina will help to evaluate the potential of tracks in distinguishing environments with similar sedimentological characteristics. In the present study area, future research will aim to further link specific vertebrate traces to coastal sub-environments to enable the definition of ichnofacies (Fig. 7). Where coastal progradation and aggradation, rather than erosion, characterizes the evolution of a particular shoreline, vertebrate tracks will be preserved, though their exposure and recovery requires special circumstances.

Track preservation

Compared to fine-grained and/or cohesive substrates, medium-to-coarse sand is considered less conducive to track preservation (Vialov 1966; Scrivner, Bottjer 1986). However, whereas trace preservation is low in loose sandy substrates (Laporte, Behrensmeyer 1980), moist beach and dune sands improve preservation potential (Van der Lingen, Andrews 1969; Ahlbrandt *et al.* 1978; Lewis, Titheridge 1978; Laporte, Behrensmeyer 1980; Lockley 1986; Loope 1986; Scrivner, Bottjer 1986; Milàn, Bromley 2006; Falkingham *et al.* 2009; Falk *et al.* 2011). Even in dunes, where deflation of the tracks and aeolian deposition of lithologically similar material greatly reduce track preservation, many aeolian tracksites have been described in the sedimentary record (McKee 1947; Brand 1979; Lockley 1986; Loope 1986; McKeever 1991; Brand 1996; Lea 1996; Milàn *et al.* 2007a, b; Roberts 2008). In high-latitude regions, such as the present study area, rapid freezing of moist track impressions at night or during winter months may also improve their preservation.

In addition to substrate conditions, the position individual tracks and especially trackways relative to bedding surfaces is an important aspect of their preservation and recovery (Figs 7B and 8). This is particularly true for bedding plane exposures where some of the most spectacular trackways have been found (Vialov 1966; Lockley 1986). Many trackways oriented along the lagoon and sea beaches of the Curonian Spit (*Bc, Ss*) run parallel to the shoreline and are analogous to bedding plane exposures in sandstones. Other tracks are oriented perpendicular to the shoreline, running up or down-dip of slightly seaward-dipping strata. These include beaver tracks (*Rc*) as well as parts of other mammalian and avian trackways upon their arrival or departure from the shoreline. Such traces may be preserved on dipping bedding planes (Figs 7B and 8). By extension, tracks found on 30–34° steep dune slipfaces are still produced in a thin package of sedimentary strata (Figs 8B and 9B, C). Given other factors conducive to preservation (moisture, rapid burial) such features have a better chance of appearing on a bedding plane or in cross-section (Loope 1986). By contrast, the tracks crossing the dipping strata of foredunes or large coastal dunes have very low preservation potential (Fig. 8A). Because episodic dune migration spans the past 5,000 years (Gudelis 1998; Bitinas 2004; Buynevich *et al.* 2007; Gaigalas, Pazdur 2008), it may be possible in the future to look at patterns of changes in biogenic structures through mid-late-Holocene by using natural dune exposures (Fig. 9C).

As mentioned above, preservation in loose sand is low, however where such tracks remain undisturbed they may be found on a single steeply dipping bedding plane. In contrast, trackways that traverse various topographic features, e.g., canine and mustelid tracks crossing the foredune ridges and moose and other tracks in the old dunes, will not be preserved

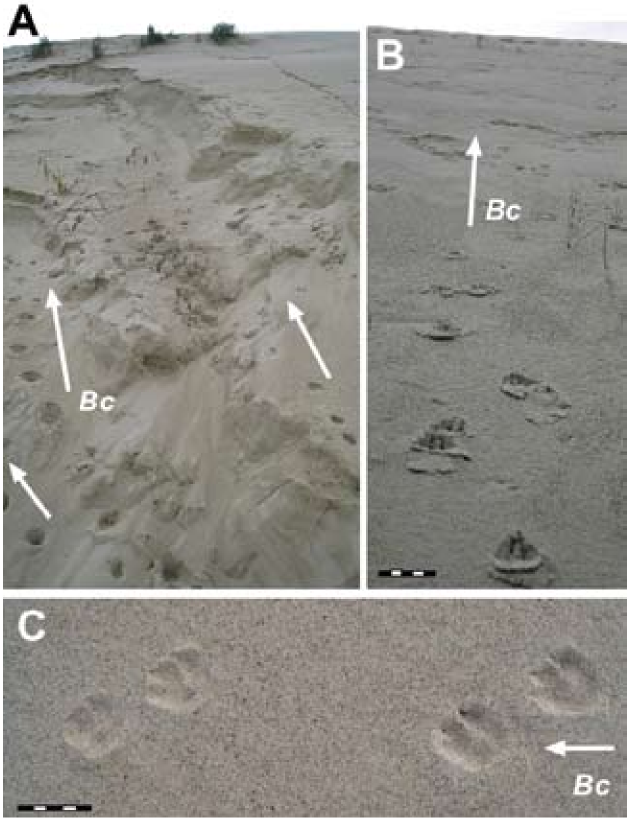

Fig. 8 Track preservation in sand. A) Several canid trackways traversing the collapsing lee face of a dune where slipface strata have been exposed by sand avalanching. Such prints will have low potential of preservation not just due to the loose nature of sand, but also due to the tracks imprinted obliquely and in different sets of slipfaces. B) Under ideal conditions, tracks produced on the slipface surface have a better chance of being preserved in a bed plane exposure or cross-section. C) *Bc* tracks in coarse sand are partially subdued as a result of deflation and infilling, but the general outlines are still visible including claw impressions. The prints are oriented parallel to the sea shoreline

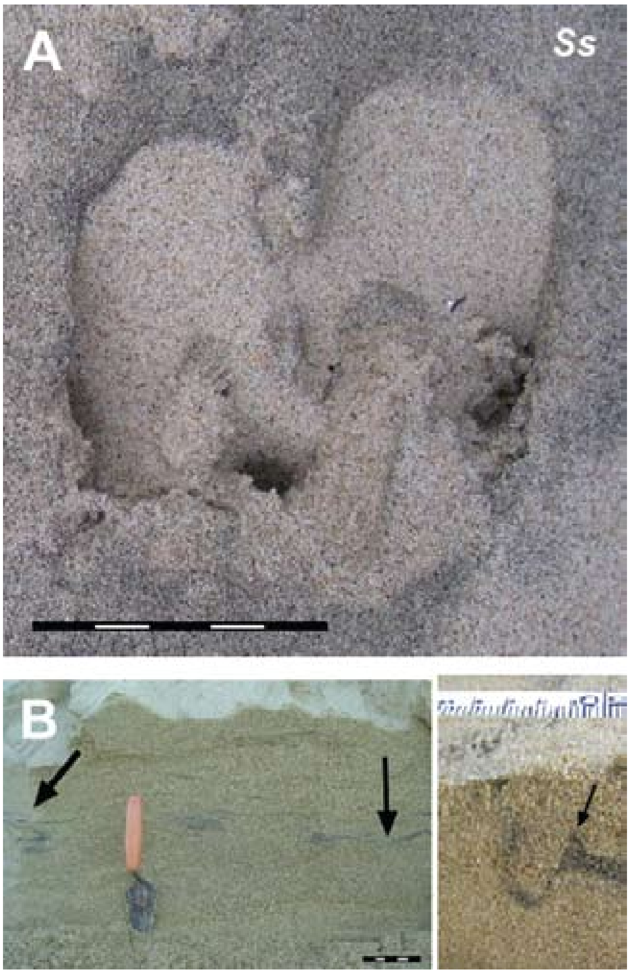

Fig. 9 A) Two partially infilled wild boar tracks (*Ss*) along the lagoon beach. The hoofprint outlines are still relatively sharp, partially due to the concentration of heavy-minerals in the moist surface sand layer. B) Cross-section of the Parnidis Dune slipface beds showing a series of concave-upward structures, which may represent physical sedimentary structures or track impressions. C) a sharp concave-up structure in a cross-section of slipface strata at Nagliu National Reserve (north of Nida). Note a raised rim on the right (arrow) that bears similarity to marginal ridges preserved in some footprints (Loope 1986; Lea 1996; Milàn *et al.* 2007a). These photos demonstrate the role of thin heavy-mineral concentrations in accentuating the geometry of the structures

on a single bedding plane. They will likely show up as isolated tracks, overprinted (direct register), or closely spaced tracks. If not covered quickly, avian and mammalian tracks along the Curonian Lagoon (Figs 5 and 6) will be likely be destroyed by shore ice, wave erosion or subsequent trampling. Nonetheless, in the long-term, many tracks formed behind the active dunes may be preserved through rapid burial by landward-moving slipfaces and avalanching (Fig. 7B). Similar to old forest floor and remains of settlements (Gudelis 1998; Bučas 2001; Buynevich *et al.* 2007), there are likely many traces of vertebrates preserved beneath the landward margin of the Great Dune Ridge (Fig. 7B).

Lithological anomalies, such as heavy-mineral concentrations often improve the recognition of tracks both in plan view and in cross-section (Fig. 9; Van der Lingen, Andrews 1969; Lewis, Titheridge 1978; Loope 1986; Buynevich 2012). Recent studies of dune stratification using ground-penetrating radar (GPR) show that heavy-mineral concentrations tend to produce strong subsurface reflections and aid in detecting biogenic structures (Buynevich *et al.* 2007; Buynevich 2011a; 2011b; Buynevich *et al.* 2011). This research demonstrates that high-frequency GPR antennas (>800 MHz) have sufficient resolution (3–5 cm) for detecting large vertebrate traces in sandy substrates, particularly where disturbed shallow sedimentary strata consist of lithologically distinct horizons.

CONCLUSIONS

A diverse suite of vertebrate footprints documented along the coast of Lithuania offers insight into the distribution and preservation potential of tracks in sandy substrates. For ease of reference to multiple tracemakers considered in this study, the classification of modern mammalian and avian tracks makes use of Vialov's (1966) nomenclature to differentiate traces produced by members of the same family, while preserving the integrity of zoological systematics. For example, while it may be difficult to distinguish between seagull and small duck prints (*Avipeda*), there is a clear difference between the webbed prints and other shorebird tracks (*Avipeda* (*Charadriipeda*)). The latter can be further subdivided based on track morphology and observation of the actual trackmaking activity.

In many sedimentary sequences, it may be difficult to identify a tracemaker to the degree possible in recent settings (e.g., small moose vs. large deer prints, beaver vs. muskrat trackways, etc.). However, the overall setting would be generally consistent, such that exact tracemaker identification would not be as important as its role as a paleoenvironmental indicator. In this respect, the Curonian Spit serves as an ideal setting characterized by a range of depositional environments serving as proffered habitats (e.g., aquatic rodents along lagoonal shoreline). With further research, it should be possible to define a series of vertebrate ichnofacies (lagoon shoreline, open sea beach, dunes, etc.) that may include other vertebrate traces (e.g., reptiles) in addition to those described here (Fig. 7).

The preservation of vertebrate tracks in sand (ichnotaphonomy) is an important issue for both interpreting fossil footprints and for locating new track sites. As shown in Fig. 8, the attitude of a trackway relative to sedimentary bedding planes will determine the final appearance of the track sequence, if preserved. Also, in addition to sand moisture and silt fraction content (Loope, 1986; not an issue in the study area), rapid freezing of the track and subsequent burial by windblown sand may facilitate its preservation in high-latitude dune settings. Finally, the present study demonstrates the role of lithological anomalies, such as heavy-mineral concentration on the periphery of tracks (Buynevich 2012), in facilitating the recognition of tracks both in plan view and in cross-section (Fig. 9). This offers a unique opportunity to identify and map vertebrate tracks using both high-resolution geophysical (GPR) imaging and trench exposures in sand-dominated coastal and aeolian sequences.

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