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Research article

Neoichnology of a Lake Margin in the Canadian Aspen Parkland Region, Cooking Lake, Alberta

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Abstract | Neoichnology provides insights essential for interpreting trace fossils in the rock record. Despite the wealth of studies conducted in marine nearshore environments, non-marine environments including lacustrine settings have received comparably little attention. Moreover, previous neoichnological studies of lakes are restricted to arid, semi-arid, tropical, and alkaline lakes, and there is a gap in knowledge of lakes in higher latitudes. The lake biome is controlled by multiple biotic and abiotic factors, and it is essential to compare lakes at different environmental settings to have a fuller understanding of lacustrine ichnology. Herein, we report on a trace assemblage comprising both invertebrate and vertebrate tracemakers in a natural lake situated within Canadian Aspen Parkland. Using detailed observations and photogrammetry, traces made by invertebrates such as fly larvae, beetles, and slugs, and (vertebrate) shorebirds are documented. Comparisons with current ichnofacies models show that these temperate latitude trace assemblages do not fully conform to the archetypal *Mermia* or *Scoyenia* Ichnofacies. For instance, fieldwork reveals a predominance of diminutive, penetrative burrows and simple surface trails that differ from the archetypal lacustrine ichnofacies. The study highlights the impact of environmental factors, such as water saturation and seasonal changes, on trace formation and preservation, providing insights into the ichnological characteristics of high-latitude lakes. These findings contribute to palaeoenvironmental interpretations and underscore the need for further research on the ichnology of forested lake systems, especially across different seasons and geographical settings.

Lay summary | Neoichnology is the study of modern animal traces (burrows, footprints, etc.) that are important in interpreting sedimentary rocks and trace fossils. Despite the wealth of studies in marine environments, there has been less research that deals with lakes. Lakes in tropical areas have been minimally studied for neoichnology in the past, and no one has conducted detailed investigations on lakes in higher latitude settings. The organisms that live in lakes, and consequently the traces that they produce, are controlled by multiple biological and environmental factors, and it is essential that we study various types of lakes to fully understand the sedimentary record of lakes. In this paper, we describe the animals and their traces that occur at a natural lake situated at the boundary of Canadian boreal forest and prairie grasslands. Through our observations, we identify traces produced by animals such as fly larvae, beetles, slugs, and shorebirds. These trace assemblages do not conform with what we have traditionally regarded as the typical trace fossil assemblages associated with lake sediments. Our findings indicate that environmental factors such as ground water content and seasonal changes play important roles in determining the types of animal traces present and their preservation. These results will contribute to a better understanding and interpreting trace fossils of ancient forested lakes in high latitudes, and also highlights the need for detailed studies in different types of lakes.

Keywords: Neoichnology; Lacustrine; *Mermia* Ichnofacies; High latitude lakes

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1. Introduction

Neoichnology provides insights essential for interpreting trace fossils in the rock record (e.g., Abel, 1935; Häntzschel, 1939; Frey, 1968, 1970; Schäfer, 1972; Ekdale & Berger, 1978; Gingras et al., 1999; Zonneveld, 2016). Some environmental settings, such as marine intertidal, have received considerable attention (e.g., Dashtgard, 2011; Dashtgard & Gingras, 2012; Baucon, 2021), due in part to ease of accessibility, whereas others remain under-studied. Although relatively easily accessed, lacustrine neoichnology has been inconsistently applied and is thus included in this latter grouping. Although lakes in some environmental settings, such as arid, semi-arid, tropical, and alkaline lakes, have received considerable attention (e.g., De Deckker, 1988; Cohen et al., 1991, 1993; Scott et al., 2007, 2009; Hamer & Sheldon, 2010; Hasiotis et al., 2012), those in other settings, such as temperate forest and grasslands, have received scant attention.

Many analyses of lacustrine bioturbation have been limited to specific groups of animals such as shield shrimps, ostracods, myriapods, and insects, in attempts to compare modern traces with fossil examples (e.g., Knecht et al., 2009; Retrum et al., 2011; Lima et al., 2017; Getty & Loeb, 2018; Sedorko et al., 2024). Chamberlain et al. (1975) and White & Miller (2008) summarised general patterns of modern animals and their traces found along lakes and lake margins. These synopses illustrated that vertebrate tracks, arthropod traces, and gastropod trails are among the most common types of traces observed in modern lakes. Despite these efforts, many previous studies did not account for the entire ecosystem, including the diversity of animals present and/or the different lake zones of natural lake systems. Additionally, detailed neoichnological studies in higher latitudes (temperate to Arctic) are still lacking.

The most common types of lakes in the modern interglacial period are glacial scour lakes, predominantly found in high-latitude areas and characterised by their relatively small sizes and shallow depths (Wetzel, 2001). Many of these lakes occur within Canadian forests partially due to relatively high precipitation and low evaporation rates (cf. Mitchell & Prepas, 1990). Yet, despite their abundance, these lakes have received very little attention in ichnological studies. One aspect of the lake biome is that they are influenced by a number of environmental variables, such as temperature, salinity, light, oxygen content, precipitation, inflow-outflow relationships and productivity, which control the types of organisms found within them (Hasiotis, 2002; Buatois & Mángano, 2009, 2011). This variability in lake characteristics and the supported biomass is not well documented, leading to a gap in understanding of tracemakers and their traces in natural lake settings compared to other sedimentary environments (cf. Scott et al., 2012). Hence, it is crucial to compare lakes at different environmental settings to have a fuller understanding of lacustrine ichnology.

In this study, we examine the types and patterns of modern animal traces, particularly those of invertebrates, around a woodland lake in Alberta, Canada. Our findings aim to; (1) identify and classify modern traces based on morphologies, (2) compare them to the ichnofacies model, and (3) enhance our understanding of animal traces in lakes within forested regions. This research contributes to palaeoenvironmental interpretations of high-latitude lakes and may be especially relevant for interpreting lake deposits from interglacial periods.

2. Study area

Cooking Lake is located about 25 km SE of Edmonton in Strathcona County, Alberta, Canada (Figure 1). It has a broad surface area but is relatively shallow, with a maximum depth of ~ 4.5 m (Mitchell & Prepas, 1990). The average lake level of Cooking Lake has decreased ~ 3 metres over the past century, coincident with decreasing net precipitation and increased net evaporation (Timoney, 2024). According to Ecological Stratification Working Group (1995), the area is situated within the Aspen Parkland Ecoregion (part of the Prairie Ecoregion), which acts as the transition between boreal forests of the north and prairie grass lands in the south. The forests in the region are dominated by aspens (*Populus tremuloides*) with abundant mixed farmland in the area. The ecoregion houses major wetlands in the Prairie Provinces (Rowe, 1987). At the local scale, the lake is surrounded by deciduous and coniferous forest. The mean annual temperature is 2.4°C with mean January temperatures of -12.3°Cand mean July temperatures of 16.2°C (Figure 2A). Mean annual precipitation is 434 mm (average between 1991 to 2020 at Edmonton International Airport, 30 km west of the lake; Environment and Climate Change Canada, n.d.) (Figure 2A). Ice cover persists from November to April (Timoney, 2024), which coincides with the months with sub-zero mean monthly temperatures.

Cooking Lake is highly productive, often leading to eutrophication during summer months (Mitchell & Prepas, 1990). Lake level is largely controlled by precipitation and evaporation, and salinity is kept at low to moderate levels (Mitchell & Prepas, 1990; Timoney, 2024). Annually, the lake levels change about 10 to 50 cm (Government of Alberta, n.d.) (Figure 2C), which, given the low gradient of the lake profile, can expose about 30 m of lake shore in late summer. Mitchell & Prepas (1990) reported average specific conductivity of 1.402 mS/cm (standard error = 0.0428 mS/cm) across six measurements taken between May to August of 1983. The brines are mainly fed through ground water discharge associated with the Devonian carbonate aquifers (cf. Michael et al., 2003; although their study was conducted further west of where Cooking Lake is situated). Lake shore sediments are predominantly subangular to subrounded fine-grained sands. Endobenthic microbial mats, colonising just below the sediment surface, provide a green to purple colouration, whereas the sediments below the mats (typically > 5 mm in depth) are

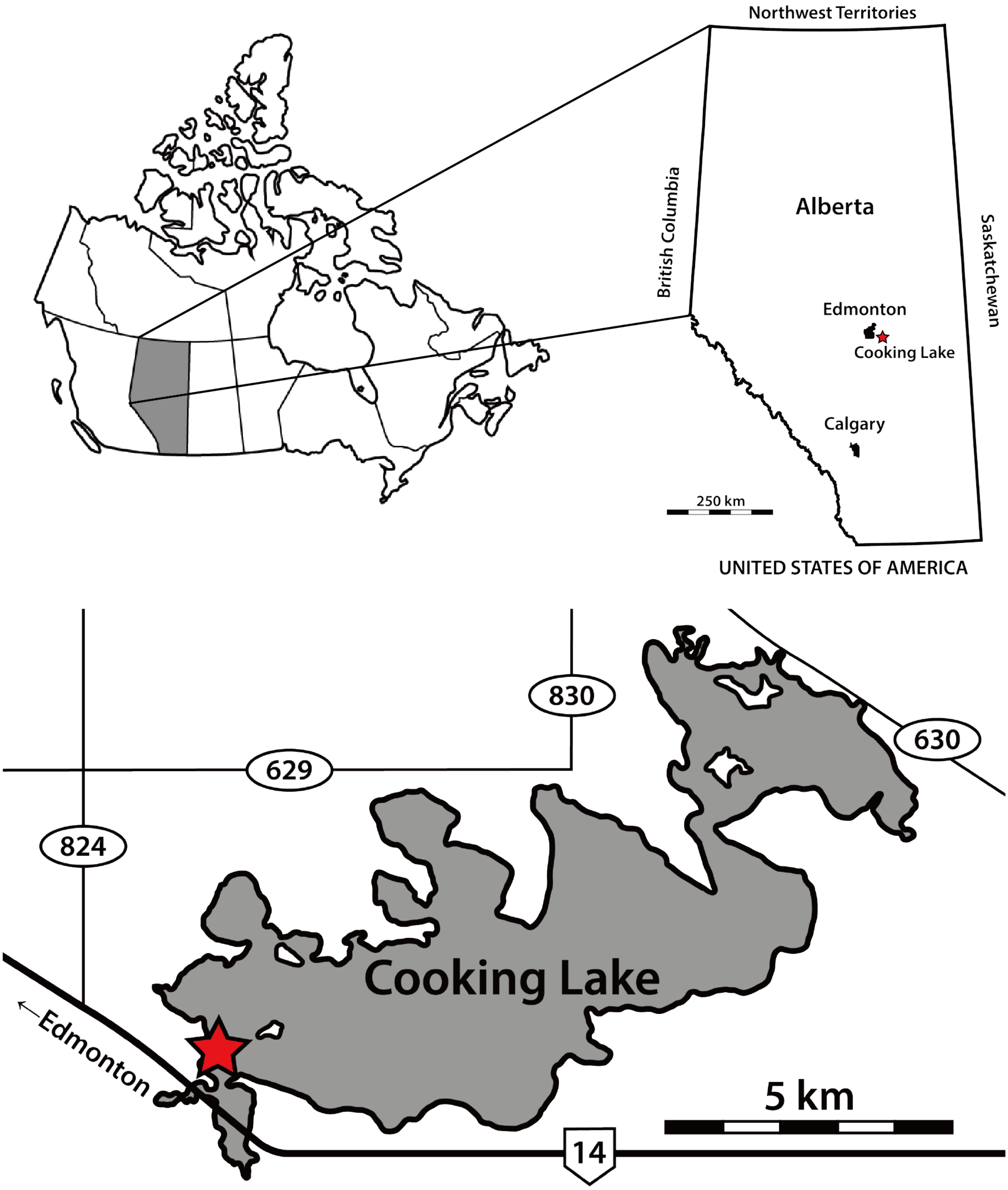

Figure 1 | Map of the study area. Cooking Lake is located in central Alberta, ~ 25 km SE of Edmonton. The study was conducted at South Cooking Lake park on the western side of the lake, indicated by the red star. The map of Cooking Lake is modified from Mitchell & Prepas (1990).

anoxic and black in colour. Subaqueous sediments are covered by a layer of silt and organic detritus that is very soft. There is sparse vegetation at the high-water mark, and sedge abundance increases away from the water's edge.

The lake, known to host a myriad of aquatic invertebrates, is an important area for breeding and resting waterfowls (Mitchell & Prepas, 1990). Frequent eutrophic episodes combined with ice coverage in winter months results in anoxia (Hickman, 1978), thus the lake cannot sustain most fish species. Gingras et al. (2007) described the burrowing behaviours related to chironomid fly larvae coping with anoxia during winter times at Cooking Lake. Local invertebrate faunal assemblages have not been reported on since the 1960s, at which time, Chironomidae larvae, amphipods, oligochaetes, Trichoptera, Hirudinea, Sphaeriidae, and hemipterans were the major constituents of the Cooking Lake benthic fauna (Kerekes, 1965). Census studies of lake margin invertebrates are not presently available whereas several studies have focussed on the vertebrate faunas in the vicinity of Cooking Lake (particularly birds) that were compiled by government sectors and citizen scientists (e.g., Kemper, 1976; Saxena et al., 1997 and references therein; Cornell Lab of Ornithology, n.d.). Cooking Lake provides a crucial stopover for migrating shorebirds utilizing the North American Central

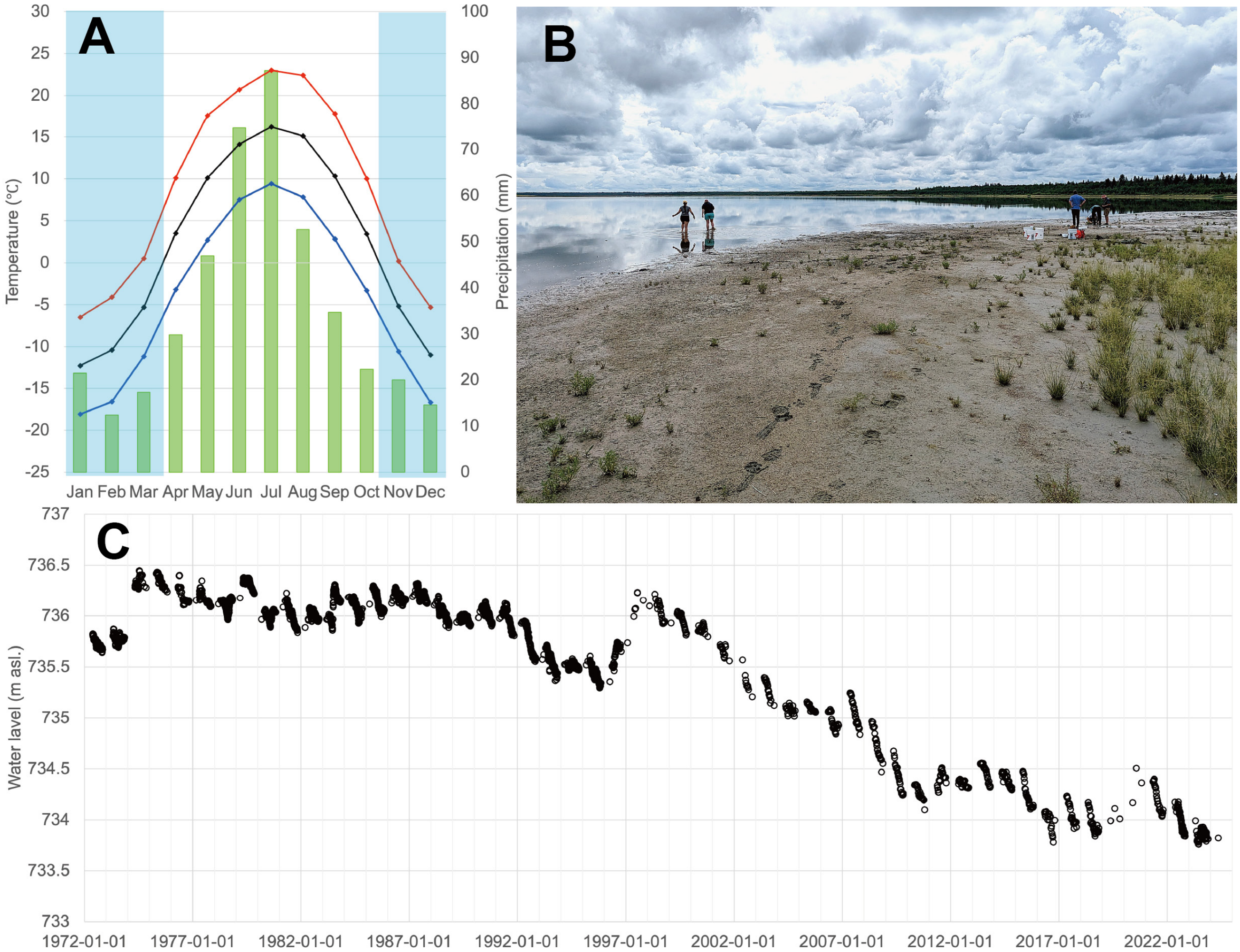

Figure 2 | Image of the lake shore and meteorological/hydrological data related to Cooking Lake. (A) Mean monthly temperature and precipitation between 1991 and 2020 at Edmonton International Airport (Environment and Climate Change Canada, n.d.-a). The lines indicate mean temperatures (red: daily maximum; black: daily average; blue: daily minimum) and the green bars show mean precipitation. The months where mean daily temperatures are sub-zero has been highlighted with light blue. (B) Image of the study area (image courtesy of Janice Kenney). (C) Graph showing water level changes at Cooking Lake between 1972 to 2024 (n=4278; Government of Alberta, n.d.). Lake levels are described in meters above sea level (m asl.). Note that the annual change in water level is approximately 10 – 50 cm.

Flyover migration route (Kemper, 1976; Mitchell & Prepas, 1990).

3. Methods

Field work was conducted in late August on the Western margin of south Cooking Lake (53.412200°N, -113.111800°W; Figure 2B). The salinity of the lake was measured to be ~2 ppt using a refractometer. Both invertebrate and vertebrate traces identified at the lake were photographed with a Canon EOS 6D Mark II mounted with EF 24-105 mm F4L lens, EF 100 mm F2.8L macro lens, and EF 70-300 mm f/4-5.6 telephoto lens. The images were then used to construct a 3D photogrammetric model on Agisoft Metashape Professional Version 1.6.5 (Agisoft LLC, 2020). These models were used to (1) produce orthogrammetric projections of the composite photoset while retaining very high data resolution, and (2) make measurements related to trace morphologies in the lab.

Invertebrates and vertebrates around the lake that were actively or potentially interacting with the substrate were observed and recorded. The substrate conditions are reported based on the water content (soupy, soft, and semi-firm), which can be determined by anatomic fidelity of bird tracks (cf. Melnyk et al., 2022): soupy substrates are water saturated with poorly defined outlines of bird tracks; soft substrates are less saturated and the deeply impressed bird tracks have well defined margins; semi-firm substrates are well drained and usually sandy, and the bird tracks (if present) are incomplete usually lacking the impression of metatarsal pads. Sediments above and below water were trenched in a square shape to approximately 10 cm depth with a shovel in order to observe any infaunal bioturbation.

Traces were classified into morphotypes based on their form and pattern of occurrence. Insects and molluscs were photographed, with some individuals being collected for identification in the lab. Invertebrate sampling was conducted by capturing and preserving them in 75% ethanol as suggested by Martin (1977). In addition to preserved samples, some live specimens of larvae were collected and reared to assist with identification. The latter was done made down to the Family level according to

Clifford (1991), Arnett Jr (2000), and Grimm et al. (2009). Vertebrates (birds) were only observed from a distance and photographed for identification. Characterization of bird traces are done following the terminologies used in Zonneveld et al. (in press-b). Where possible, the vertebrates were identified down to the species level according to Fisher & Acorn (1998).

4. Results

4.1. Invertebrates observed

In terms of diversity and abundance, fly larvae (Insecta: Diptera) are the most common invertebrates found at the lake site. Larvae of biting midges (Ceratopoginidae; Figure 3A) and non-biting midges (Chironomidae; Figure 4A) are found within fully subaqueous sediments, whereas soldier flies (Stratiomyidae; Figure 3B) and crane flies (Tipulidae; Figure 3C) are present in sediments above water level. Additionally, several fly pupae were collected from subaerial sediments, which were later identified as shore fly pupae (Ephydridae; Figure 3D) following their rearing in the lab. An unidentified dipteran larva (similar to Muscidae larvae; Figure 3E) was also collected from shore sediments along with Stratiomyidae and Tipulidae larvae.

Other insects found on the lake shores include both adult and larval variegated mud-loving beetles (Heteroceridae; Figure 4H-I), a winged individual (i.e., male or queen) of an unclassified ant (Formicidae; Figure 5A), and a caterpillar of the banded tiger moth (Arctiidae; Figure 5C). As for non-insect invertebrates, ostracods of unknown species (Crustacea: Ostracoda; Figure 4B) were found in subaqueous bottom sediments, and field slugs belonging to *Deroceras* sp. (Mollusca: Gastropoda; Figure 3F) were found traversing vegetated lake shores.

4.2. Invertebrate traces

Cooking Lake presents various types of burrows and trails left by invertebrates at different distances with respect to the high-water mark of the lake. These traces were classified into 9 morphotypes (Table 1):

Trace Morphotype	Description	Position at the Lake	Similar Trace Fossils	Tracemakers (potential tracemakers)
Invertebrate Burrows				
Morphotype I	Unfilled, U-shaped and inclined burrow. ~ 1.5 mm in diameter. Burrow lined by mucus.	Fully submerged	U-shaped: *Arenicolites* Inclined: *Arenicolites* or *Skolithos*	Chironomidae
Morphotype II	Unfilled, unlined, U-shaped, Y-shaped, and boxwork burrows. ~ 0.5 mm in diameter.	Fully submerged	U-shaped: *Arenicolites* Y-shaped: *Polykladichnus* Boxwork: unassigned	(Ceratopogonidae, Ostracoda)
Morphotype III	Unfilled, unlined, unbranched, straight to slightly meandering burrows. ~ 2 mm in diameter. Restricted close to the surface. Some burrows transition into trails of Morphotype IX.	Above water level on wet sediment	*Helminthoidichnites*	(Ephydridae, Stratiomyidae, Tipulidae)
Morphotype IV	Unfilled, unlined, occasionally branching, irregularly meandering burrows. 1-2 mm in diameter. Found in the subsurface and penetrates down to the anoxic layer.	Well above water level	?*Helminthoidichnites* (If not branching)	(Ephydridae, Stratiomyidae, Tipulidae)
Morphotype V	Unfilled, unlined, branching, irregularly meandering burrows. Branches are usually short but can be elongated in some burrows. ~ 5 mm in diameter (2.5 mm inner diameter and 1.25 mm burrow wall). Restricted to the surface and does not change in depth.	Well above water level, close to vegetation	*Paracanthorhaphe*, *Labyrintichnus*	Heteroceridae
Invertebrate Trails				
Morphotype VI	Elongated furrow of equal width (~ 5 mm), no distinct lateral or medial rideges, winding and meandering but does not self-cross.	At water's edge on soupy sediments	*Helminthopsis*	Formicidae
Morphotype VII	Elongated bilobate furrow of equal width (8-10 mm), lateral ridges on both sides, may have faint median ridge, straight overall and meanders only slightly, does not loop.	At water's edge on soupy sediments	*Aulichnites*	Arctiidae
Morphotype VIII	Elongated furrow of equal width (5-7 mm), associated with lateral ridges on both sides, straight to irregularly meandering but does not loop.	Above water level	*Archaeonassa*	(Agriolimacidae, Arctiidae)
Morphotype IX	Elongated furrow of equal width (1-2 mm), straight to slightly meandering or curved and may loop occasionally, some trails transitions into burrows of Morphotype III.	Above water level, common on wet sediments	*Helminthoidichnites*	(Ephydridae, Stratiomyidae, Tipulidae)

Table 1 | Invertebrate traces found along Cooking Lake. Each trace morphotype is described for their morphologies and occurrences, similar trace fossils, and their tracemakers. Where there is no direct evidence of trace-tracemaker relationships, the potential tracemakers are indicated in brackets.

Figure 3 | Invertebrates occurring at Cooking Lake. All of the invertebrates are oriented with their heads towards the left of the diagram, and the scale bars represent 5 mm. (A) Larvae of Ceratopogonidae. The larvae were all found underwater. The strong brown coloration is due to ethanol used to preserve the larva, and it was a paler colour when alive. (B) Larvae of Stratiomyidae. (C) Larvae of Tipulidae. (D) Adult Ephydridae reared from pupae collected at the lakeshores. (E) Unidentified fly larvae. The form is similar to that of Muscidae. (F) Agriolimacidae.

Morphotype I:

Morphotype I are found 5 - 10 cm under water in soupy substrates and consist of incipient *Arenicolites* and *Skolithos* (Figure 4A-B). The burrows have a diameter of around 1.5 mm and penetrate down about a 1 cm into the substrate. The internal walls of these burrows are smooth and stabilised by mucus. These burrows were commonly associated with chironomid larvae.

Morphotype II:

Morphotype II are also found under water and include incipient *Arenicolites*, *Polykladichnus*, and boxwork burrows (Figure 4A-B). These burrows are smaller than Morphotype I, with a diameter of <0.5 mm and penetration depth < 1 cm. Additionally, the U-shaped burrows can be highly asymmetrical (skewed) and unlined, which are attributes not observed in Morphotype I. Ostracods were observed within these burrow systems (Figure 4B), although they were not observed actively constructing these burrows.

Morphotype III:

Morphotype III are found on soft to semi-firm substrates just above the high-water line and consist of burrows that are unbranched, unfilled, unlined, and straight to irregularly winding (incipient *Helminthoidichnites*). They are approximately 2 mm in diameter, and are highly abundant, often crossing each other or grading in and out of the sediment to form narrow surface tails (Morphotype IX) with a width of about 1 mm (Figure 4C). The burrows are also restricted to the surface resulting in a positive epirelief structure.

Morphotype IV:

Morphotype IV are found well above the water's edge on semi-firm substrates. They have similar morphologies to Morphotype III, and include unlined, unfilled, and irregularly winding burrows (incipient *Helminthoidichnites*?) with diameters of 1-2 mm. In contrast to the surficial nature of Morphotype III, Morphotype IV are more deeply penetrating (to about 5 cm) and exhibit branching, false branching, or secondary successive branching (cf. D'Alessandro & Bromley, 1987; Figure 4D). Some of the burrows reaching the anoxic layers have a halo of oxidised sediments around the burrow walls (Figure 4D).

Morphotype V:

Morphotype V are found on the beach in well-drained, semi-firm substrates in vegetated areas. These are surficial burrows and are highly branched, unfilled, and straight to meandering (incipient *Paracanthorhaphe* and *Labyrintichnus*, see section 5.1; Figure 4E-F). In cross-sectional views, the burrows are found restricted to the upper surface where cyanobacterial mats are present and are constructed by displacing the surface sediments to the top which acts as the ceiling (Figure 4G). Burrow diameters are larger than the ones described earlier with an inner diameter of about 2.5 mm, with the ceiling walls reaching 1.25 mm in thickness. The branches are usually short, but they can become extensive with secondary branchings; one burrow was found having a total length of about 1.4 m with 9 nodes (Figure 4F). Some of the burrows were found with larvae and adults of Heteroceridae residing within them (Figure 4H-I). In general, larval burrows are larger and better developed compared to adult burrows.

Morphotype VI:

Morphotype VI are found on soupy substrates at the water's edge. These are elongated epichnial furrows of equal width (~ 5 mm) that do not possess any distinct lateral or medial ridges (Figure 5A-B). The burrows are strongly winding and meandering but do not self-cross (incipient *Helminthopsis*; Figure 5B). Such trails were observed being actively produced by a winged ant (Figure 5A). The ant was partially burying its head and thorax into the substrate, constructing the trail with a bulldozing motion.

Morphotype VII:

Morphotype VII are found in wet, soupy substrate at the water's edge. These are trails that possess lateral ridges on both sides and an occasional, faint median ridge (incipient *Aulichnites*; Figure 5C-D). The courses are straight to sinuously meandering, but they do not form loops. They have a consistent width of about 8–10 mm and are larger compared to other trail morphologies. During the study, they were observed being produced by banded woolly bear caterpillars traversing along the shores (Figure 5C).

Morphotype VIII:

Morphotype VIII are surficial trails found above the water level on soft to semi-firm substrates occurring between the high-water mark and the vegetated areas. They are slightly smaller than Morphotype VII, with a width of 5–7 mm. They completely lack a median ridge (incipient *Archaeonassa*; Figure 5E). These trails are usually straight to irregularly meandering.

Morphotype IX:

Morphotype IX are found above the water level but are most frequent on wet, soft sediments close to the shoreline. These are narrow, elongated furrows with a consistent width of approximately 1 mm. They display irregular curves and meanders, occasionally forming loops (incipient *Helminthoidichnites*; Figurse 4C and 5E). Some trails are apparently connected to burrows of Morphotype III and were likely produced by the same tracemaker (Figure 4C).

4.3. Vertebrate tracemakers

Birds are the only vertebrates observed during this study. Except for a few dabbling ducks, these birds can be grouped into shorebirds (Charadriiformes). The birds were identified as Baird's sandpiper (*Calidris bairdii*; Figure 6A), Stilt sandpiper (*Calidris himantopus*; Figure 6B), Long-billed dowitcher (*Limnodromus scolopaceus*; Figure 6C-D), Lesser yellowleg (*Tringa flavipes*; Figure 6B, E), Greater yellowleg (*Tringa melanoleuca*; Figure 6F), and an unidentified species of dabbling duck (*Anas* sp.; Figure 6G). All the birds occupied shallow lake waters but are likely present on the shores when humans are not around. American avocets (*Recurvirostra americana*; Figure 6H) were also found near the centre of the lake basin away from the shores.

4.4. Vertebrate traces

Various types of vertebrate traces were also observed, including tracks, trackways, and trampling marks found along the lake margins (Figure 7A-B). The individual tracks range in print lengths of 2-6 cm (mostly 2-3 cm), with print widths measuring between 2-5 cm (the majority being 3-4 cm). The angle between digits II and IV ranges from 65° to 153°, with the majority falling between 100° to 120°. Most tracks were incumbent anisodactyl (tridactyl; incipient *Koreanaornis*), although some clearly show anisodactyl (tetradactyl) patterns with impressions of the posteriorly-directed digit I (hallux) preserved (incipient *Ardeipeda*). Webbing was only observed in one palmate trackway (incipient cf. *Presbyornithiformipes*; Figure 7A). It is interesting to note that, while the overall morphology of the non-webbed tracks is consistent across the study

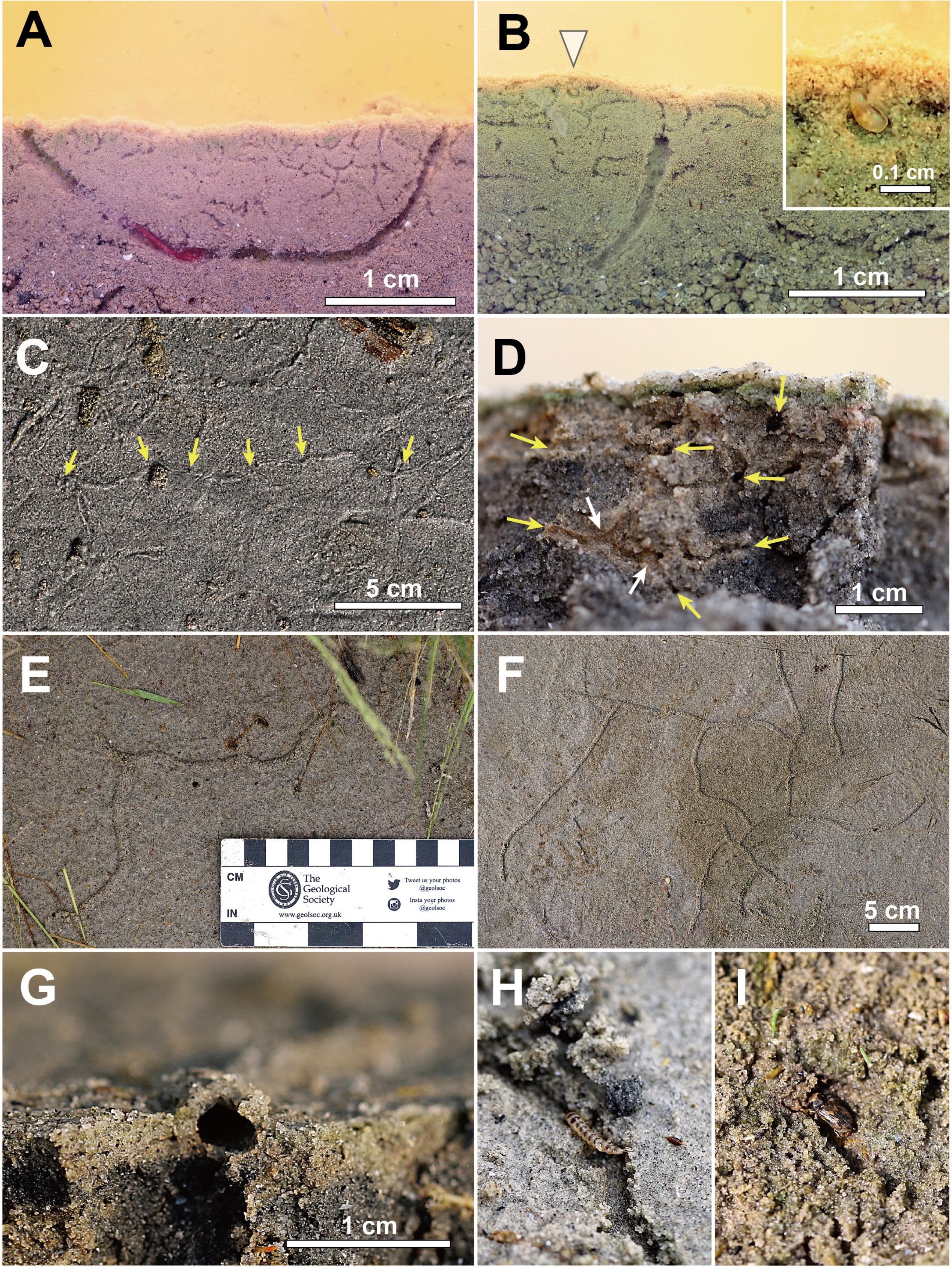

Figure 4 | Invertebrate burrows at Cooking Lake. (A, B) Morphotype I and II found underwater. Burrows of Morphotype I are larger and include shaft or U-shaped (incipient *Skolithos* and *Arenicolites*), whereas Morphotype II burrows are small and may be U-, Y-shaped (incipient *Arenicolites* and *Polykladichnus*), or boxworks. Notice the Chironomidae larvae at the base of the U-shaped Morphotype I in A and the ostracod in the substrate in B (indicated by a white triangle with a blow-up on top right). (C) Burrows of Morphotype III and trails of Morphotype IX (incipient *Helminthoidichnites*). Some burrows transition into trails (indicated by yellow arrows). (D) Morphotype IV (incipient *Helminthoidichnites*) occurring under the biomats. Burrow ends are indicated by yellow arrows. The burrows at the surface are straight but the deeply penetrating burrow shows intricate branching patterns (the nodes are indicated by white arrows). (E, F) Morphotype V (incipient *Paracanthorhaphe* and *Labyritichnus*) produced by Heteroceridae larvae. Most burrows were relatively small with few short branches (E) but they can get large with a complex network of burrow shafts (F). (G) Cross sectional view of the Heteroceridae burrow. Notice how the burrow is restricted to the biomat layer. (H, I) Larvae (H) and adult (I) Heteroceridae in their burrows. The ceiling of the burrow has been removed to expose the tracemaker.

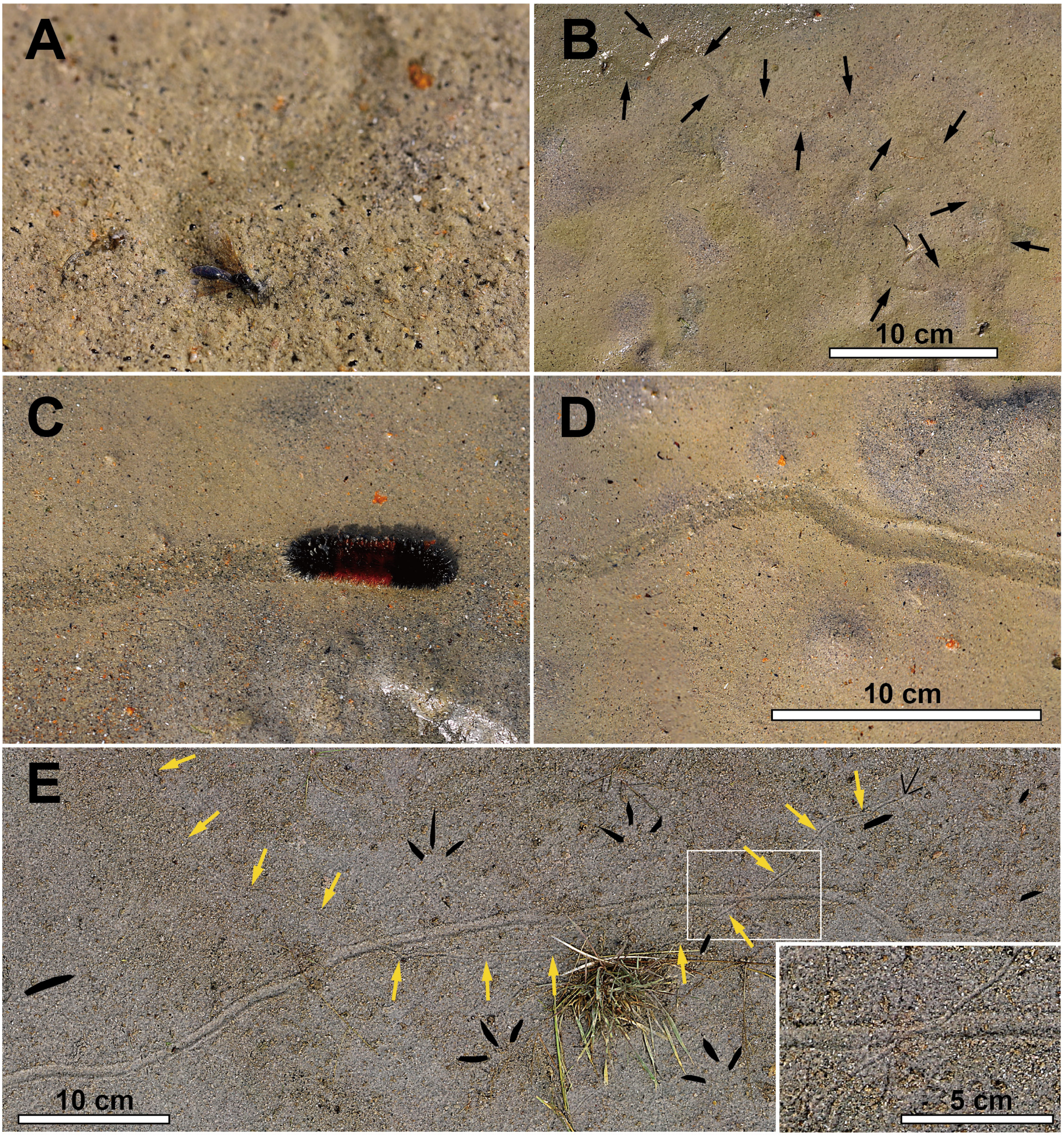

Figure 5 | Surface trails made by invertebrates. (A, B) Morphotype VI (incipient *Helminthopsis*) produced by a winged Formicidae. The trails are indicated by the black arrows with the tracemaker moving from bottom centre to the top left of the image. (C, D) Morphotype VII (incipient *Aulichnites*) produced by Arctiidae. Notice the lateral furrows and faint medial furrow of the trail. Tracemaker moved from left to right of the image. (E) Morphotype VIII (incipient *Archaeonassa*) trail crosscut by Morphotype IX (incipient *Helminthoidichnites*). The course of Morphotype IX is indicated by yellow arrows, and bird tracks are infilled in black. One of the intersections are blown-up on the bottom right.

area, the digit impressions in tracks formed in drier, firmer substrates do not converge (Figure 5E), unlike those in wetter, softer substrates (Figure 7B). While isolated tracks can be found throughout the study site, trample grounds (*sensu* Zonneveld et al., in press-b) are found just above the high-water mark in moist, soft substrate (Figure 7B). By contrast, identifiable trackways in soupy substrates are found at or directly below the high-water mark (Figure 7A).

Foraging traces are also identified throughout the locality (Figure 7C-E). Probe marks, approximately 5 mm in diameter and penetrating 1.5 cm into the substrate (Figure 7C), are observed either in isolation, aligned, or clustered. Some traces appear as paired probes from the upper and lower beaks of birds with partially open beaks. Although birds probed both above and below the high-water mark, these traces could only be observed above the waterline in soft to semi-firm substrates. Aligned probing traces, typically found higher above water, consist of multiple probings that may follow invertebrate burrows (Figure 7D). Clustered probings, sometimes with up to 15 probings per 1 cm^2, are found along the lake margins (Figure 7B, E). Most shorebirds, except *Recurvirostra americana*, were observed probing sporadically as they moved along the shore (Figure 6E). *Limnodromus scolopaceus* were also observed engaging in stitching behaviour, where the bird remains in place and continuously probes sideways without raising its head (*sensu* Angarita-Báez & Carlos, 2024; Figure 6D).

5. Discussion

5.1. Comparison with lacustrine ichnofacies

Ichnofacies related to lacustrine environments include the *Mermia* Ichnofacies in low energy, fully aquatic settings; *Scoyenia* Ichnofacies on occasionally flooded surfaces; *Coprinisphaera* Ichnofacies in fully terrestrial settings; and continental *Skolithos* Ichnofacies (albeit generally limited to *Skolithos* or *Arenicolites* e.g., Bromley & Asgaard, 1979; Sodré et al., 2023) in high energy environments (Buatois & Mángano, 2004; Scott et al., 2012). The study area is a low-energy lakeshore environment that is fully submerged or periodically inundated, with considerable groundwater influence; fully subaerial settings were not studied as they were modified into access trails. Consequently, the fully subaqueous suites are expected to include animal traces similar to the *Mermia* Ichnofacies, whereas the subaerially exposed shores should resemble the *Scoyenia* Ichnofacies. The archetypal *Mermia* Ichnofacies consist of horizontal to subhorizontal grazing and feeding structures with subordinate locomotion traces (e.g., *Cochlichnus*, *Gordia*, *Hamipes*, *Helminthopsis*, and *Vagorichnus*; Buatois et al., 1996; de Gibert et al., 2000). By contrast, the *Scoyenia* Ichnofacies features meniscate burrows and various locomotion traces left by invertebrates and vertebrates, with occasional simple horizontal and vertical burrows (e.g., *Diplichnites*, *Gruipeda*, and *Taenidium*; Kim et al., 2005; Melchor et al., 2006; de Gibert & Sáez, 2009). The distribution of modern animal traces at Cooking Lake is depicted in Figure 8.

The animal traces observed in fully subaqueous settings at Cooking Lake greatly differ from the archetypal *Mermia* Ichnofacies. These traces mainly consist of incipient *Arenicolites*, *Polykladichnus*, *Skolithos*, and unassigned boxwork burrows (Figs. 4A-B, 8). This prevalence of penetrative burrows is superficially similar to the continental *Skolithos* Ichnofacies (Scott et al., 2012). However, the vertical burrows and boxwork burrows at Cooking Lake are associated with deposit-feeding activities of the tracemakers, behaviours that align more closely with the *Mermia* Ichnofacies in an ethological sense. For example, many chironomids, the primary tracemaker of the Morphotype I burrows (incipient *Skolithos* and *Arenicolites*), feed on detritus by protruding through the burrow walls or emerging from their burrows (Berg, 1995; Charbonneau & Hare, 1998; Osborne et al., 2000). Similarly, the sizes suggest that ostracods, which are primarily deposit feeders (Karanovic, 2012), are likely to be responsible for the Morphotype II burrows (incipient *Arenicolites*, *Polykladichnus* and boxwork burrows). This contrasts with marine settings where the *Skolithos* Ichnofacies are primarily produced by suspension feeders which use high wave energy to suspend food particles (MacEachern et al., 2012). Although vertical burrows are a key feature of the *Skolithos* Ichnofacies, they tend to be deeply penetrating or exhibit adjustment structures (spreiten) to cope with high sedimentation and erosion rates (MacEachern & Bann, 2008), unlike the diminutive burrows observed at Cooking Lake. Moreover, structures produced by mobile organisms are rare in the archetypal *Skolithos* Ichnofacies, whereas the abundance of boxwork burrows at Cooking Lake suggests otherwise. Hence, simply ascribing occurrences of vertical burrows to the *Skolithos* Ichnofacies is misleading and could lead to incorrect interpretations of the depositional environment.

U-shaped and J-shaped (inclined) burrows of chironomids have been reported in various lake settings (McLachlan & Cantrell, 1976; McLachlan, 1977; McCall & Trevesz, 1982; Scott et al., 2009). Their significance to the *Mermia* Ichnofacies have been discussed extensively (Gingras et al., 2007; White & Miller, 2008; Hasiotis et al., 2012). Additionally, similar burrows in littoral sediments can be produced by oligochaetes, ephemeropterans, trichopterans, and megalopterans (Charbonneau & Hare, 1998; White & Miller, 2008), implying that this burrowing behaviour is not unique to chironomids. Fossil examples of penetrative burrows from lacustrine successions include abundant *Arenicolites* and *Polykladichnus* from the Triassic Malmros Klint Member in Greenland (Bromley & Asgaard, 1979); unassigned backfilled boxwork burrows ("tangle-patterned small burrows") from Tertiary saline lake deposits in Spain (Rodríguez-Aranda & Calvo, 1998); *Polykladichnus* also from Tertiary saline lake deposits in Calatayud-Teruel basin in Spain (Uchman & Álvaro, 2000); *Arenicolites* from the Eocene Green River Formation in the USA (Bohacs et al., 2007); diminutive boxwork burrows from the Triassic Madygen Formation in Kyrgyzstan (Voigt & Hoppe, 2010); and *Arenicolites* from the Eocene Uinta and Duchesne River Formations in the USA (Sato et al., 2018). *Arenicolites* have also been reported from floodplain mud deposits in the Upper Cretaceous Candeleros Formation of Argentina (Heredia et al., 2020).

Scott et al. (2012) suggested that, with additional evidence, the occurrence of diminutive vertical burrows in lacustrine settings could be treated as a distinct ichnofacies or a subdivision of the *Mermia* Ichnofacies. Based on our observations at Cooking Lake, we support this view. Although there are some overlaps with the *Skolithos* Ichnofacies in terms of constituent trace fossils, the vertical burrow-dominated *Mermia* Ichnofacies can be recognized by the predominance of shallow and diminutive structures, as well as the presence of mobile deposit-feeding

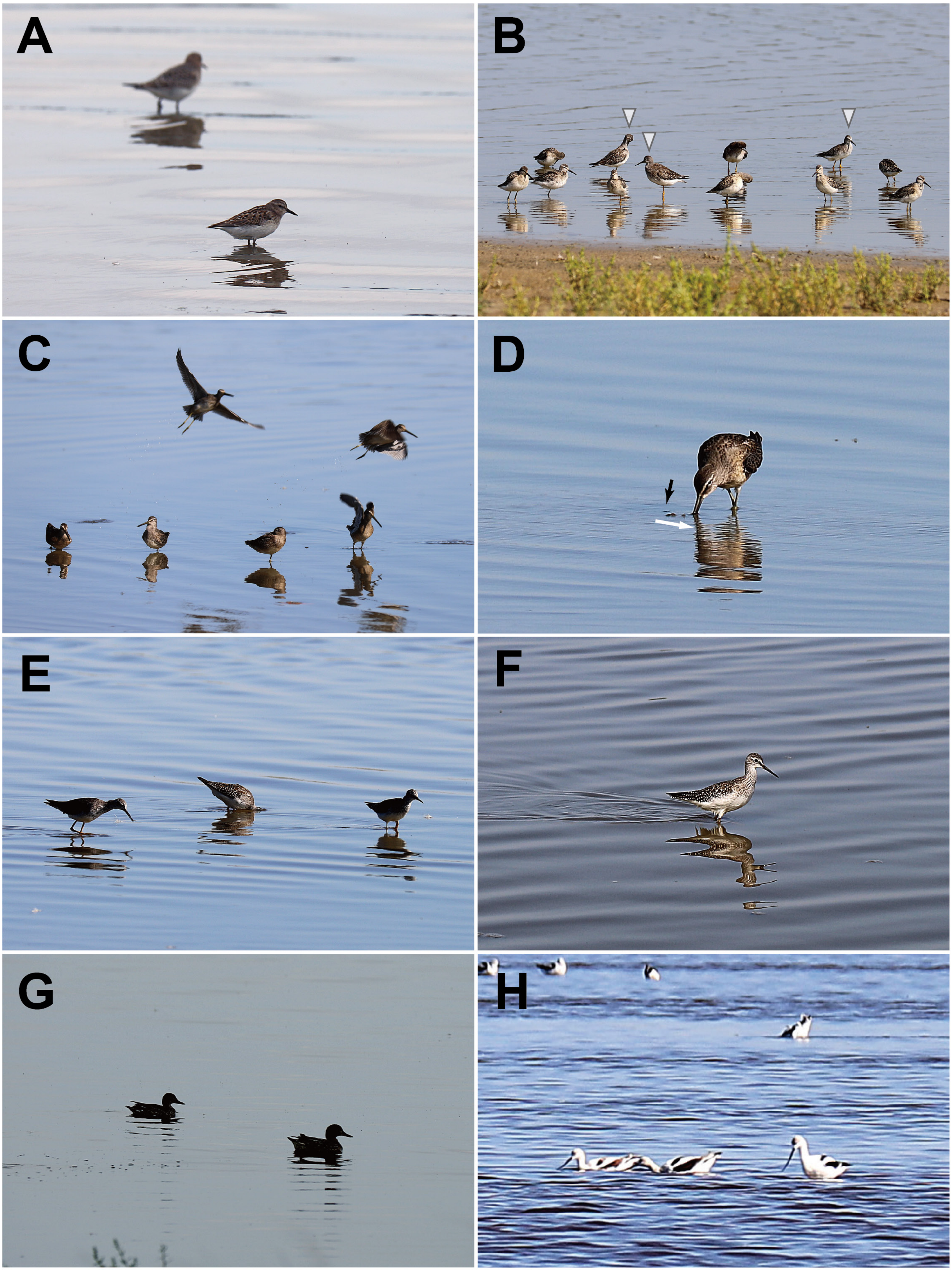

Figure 6 | Shorebirds of Cooking Lake. (A) Barid's sandpiper (*Calidris bairdii*). (B) Flock of Stilt sandpiper (*Calidris himantopus*) and Lesser yellowlegs (*Tringa flavipes*). *T. flavipes* are indicated by white triangles above their heads. The two can be distinguished by the plumage colour and the bright yellow legs of *T. flavipes*. (C) A flock of Long-billed dowitcher (*Limnodromus scolopaceus*). (D) *L. scolopaceus* engaged in stitching behaviour. Notice the sediment mound forming as the bird moved its beak from the starting point (indicated by black arrow) in the direction of the white arrow. (E) Three *T. flavipes* walking along shallow waters. The individual in the middle is probing into the substrate as it progresses. (F) Greater yellowleg (*Tringa melanoleuca*) walking in shallow waters. This individual was observed probing as it was walking. (G) Unidentified species of dabbling duck (*Anas* sp.). (H) American avocets (*Recurvirostra americana*) found in a distance, near the centre of the lake basin.

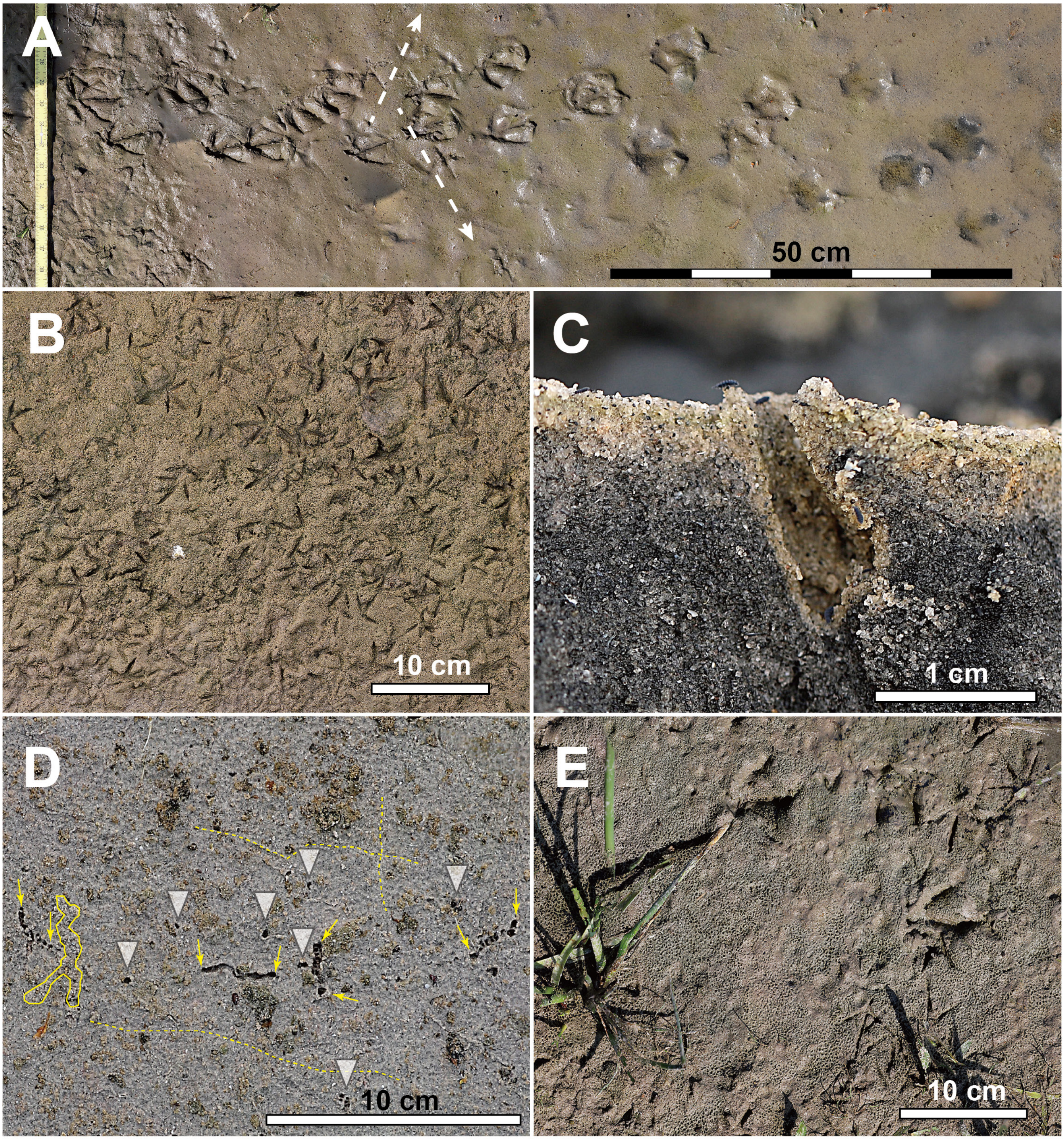

Figure 7 | Traces left by vertebrates. (A) Trackway of ducks and shorebirds (incipient cf. *Presbyornithiformipes*). The trackway going from left to right of the image is left by at least two individuals. Notice how the shape of the tracks become indistinct as the bird moved from drier shore to wet and soupy substrate. Two other trackways occur near the centre of the image, and the directions are indicated by white arrows. (B) Trampling marks left by shorebirds (consisting of incipient *Koreanaornis* and *Ardeipeda*). Abundant probings can also be found. (C) Cross-sectional view of a probe mark. Small, black insects in the image are springtails that were abundant at Cooking Lake. (D) Stitching traces (with the terminus indicated by yellow arrows) and isolated probings (noticeable probe marks are indicated by white triangles). Notice the row of beak marks at the base of stitching traces. Burrow of an adult Heteroceridae (Morphotype V) is encircled by a yellow line and surface trails (Morphotype IX) are highlighted in yellow dashed lines. (E) Clustered probing marks. The probings are associated with shorebird tracks.

structures (e.g., boxwork burrows) in planar-bedded sand to siltstone. While some may argue that incorporating sedimentological attributes to distinguish an ichnofacies diminishes the concept's inherent value, the range of sedimentological interpretations for cross-bedded sandstone and planar-bedded sand to siltstone do not overlap. Therefore, sedimentology can effectively facilitate the differentiation between the *Skolithos* Ichnofacies and the vertical burrow-dominated *Mermia* Ichnofacies. Indeed, sedimentological interpretations are normally used to inform ichnofacies interpretations as they provide the basis for integrating sedimentary processes and conditions with animal behaviours (i.e., trace fossils).

Subaerial parts of lacustrine shorelines that are frequently flooded are characterised by the *Scoyenia* Ichnofacies, which includes meniscate backfill burrows, and arthropod and vertebrate tracks/trackways/trails (Buatois & Mángano, 1995; Scott et al., 2012). In addition, shallow-tier vertical and horizontal burrows, simple surface trails, and boxwork burrows may also be present. At Cooking Lake, vertebrate tracks and shallow-tier horizontal to subhorizontal arthropod burrows (incipient *Helminthoidichnites* and *Labyrintichnus*/*Paracanthorhaphe*) are extremely common (Figures 4D-G and 5E), fitting the criteria of the *Scoyenia* Ichnofacies. However, there are striking differences between the traces found at Cooking Lake and those at other modern lake shores, notably the lack of trace diversity and the predominance of simple and diminutive traces. For example, most modern lake shores feature back-filled and/or ornamented burrows (Scott et al., 2007, 2009; Hamer & Sheldon, 2010; Hasiotis et al., 2012), which are absent at Cooking Lake. Although vertical burrows are common in other lake settings, the sediments at Cooking Lake are devoid of vertically oriented structures, except for shallow probings. While it is not uncommon for the namesake components of an ichnofacies to be absent from a given depositional setting (MacEachern et al., 2012), the complete lack of backfilled burrows is unusual. Several factors could explain this discrepancy. One is the relatively high-latitude setting of Cooking Lake that may result in lower faunal diversity. However, several species of beetles, such as ground beetles, tiger beetles, and scarab beetles, which commonly produce backfilled and vertical burrows in nonmarine settings (cf. Chamberlain, 1975; Ratcliffe & Fagerstrom, 1980), are found in central Alberta (Niemelä et al., 1992; Acorn, 2001; Floate & Kadiri, 2013). Another possible reason is the higher water content of the substrate at Cooking Lake. Previous studies have focused on lakes in arid to semiarid areas, where the eulittoral zones (subaerial zones that are seasonally inundated) are extensive. On the other hand, Cooking Lake does not experience significant drying, and its shores remain wet or frozen throughout the year, with seasonal water level fluctuations typically <40 cm (Mitchell & Prepas, 1990). In addition, the saturated sediments support microbiome growth, leading to anoxic layers from decaying organic matter beneath the surface (Figures 4G and 7C). This anoxic layer may inhibit animals from penetrating deeper into the substrate. Indeed, in continental settings, climate and groundwater profiles significantly influence the depth, diversity, and abundance of organisms (e.g., Hasiotis 2002, 2007; Hasiotis et al., 2012).

It is important to note that the ichnogenera associated with the horizontal burrows at Cooking Lake do not correspond to those typically included in the models for the *Scoyenia* Ichnofacies (e.g., *Planolites*, *Palaeophycus*, *Spongeliomorpha*, and subordinate occurrences of *Vagorichnus* and *Treptichnus*; Scott et al., 2012). This is probably due to the subtle morphological differences observed in the burrows at Cooking Lake compared to those in previous studies. For example, burrow Types III and IV are morphologically similar to *Planolites* (simple horizontal burrows), but due to the absence of active fills, we have assigned them to incipient *Helminthoidichnites* (*sensu* Buatois et al., 1998; Figure 4C-D). Similarly, the branching patterns observed in burrows of Morphotype V (incipient *Paracanthorhaphe* and *Labyrintichnus*; Figure 4E-F) bear a superficial resemblance to *Vagorichnus*. While Heteroceridae burrows have historically been classified as incipient *Vagorichnus* (Scott et al., 2007), the strict definition of the ichnogenus requires the presence of three-dimensional networks and active filling (Buatois et al., 1995), features not found in the Cooking Lake burrows. There are several other ichnotaxa that has been compared to modern Heteroceridae burrows, such as *Palaeophycus* and *Planolites* (Clark II & Ratcliffe 1989), *Steinichnus* or *Spongeliomorpha* (Hasiotis et al., 2012), and *Steinichnus*-like forms (Wang & Hu, 2014). However, we believe the burrows at Cooking Lake more closely resemble *Paracanthorhaphe* (winding burrows with short branches as in Figure 4E; cf. Buatois et al., 1996) and *Labyrintichnus* (extensive burrows forming networks as in Figure 4F; cf. Uchman & Álvaro, 2000; Uchman et al., 2017).

Avian tracks are distributed along lake shores, with higher concentrations found closer to the water's edge, though not within the water itself (see Figure 7A-B). This distribution is primarily influenced by the firmness of the substrate, which is controlled by water and organic-matter content (cf. Genise et al., 2009; Melnyk et al., 2022). Firm substrates resist deformation by the trace-making organisms, thus preserving their tracks, whereas softer substrates are unable to support the weight of the organism without being deformed (Falkingham et al., 2011). Additionally, foraging traces are observed along the lake's margins (Figure 7C-E). At present, these traces are not classified within the archetypal *Scoyenia* Ichnofacies. This is probably because ichnological studies pertaining to bird foraging are still in their infancy (Zonneveld et al., in press-a, in press-b). Although there is increasing fossil evidence of avian foraging in terrestrial sediments, their relationship between these traces and depositional environments remains underexplored (e.g., Genise et al., 2009; Falk et al., 2010; Melchor et al., 2012; Abbassi et al., 2016; Rojas-Manriquez et al., 2023; Zonneveld et al., in press-a). With additional data into the distribution of these foraging traces along both contemporary and ancient lake margins, it is possible that they could eventually be recognized as part of the *Scoyenia* Ichnofacies.

The transition zone between fully subaqueous and subaerial suits, such as shorelines, is characterised by diminutive arthropod trails (Morphotypes VI, VII, and IX; incipient *Helminthopsis*, *Aulichnites*, and *Helminthoidichnites*, respectively), shallow burrows, and occasional avian trackways (Figures 4C and 5A-D). This zone is only about a metre in the lake's transect direction but contains a

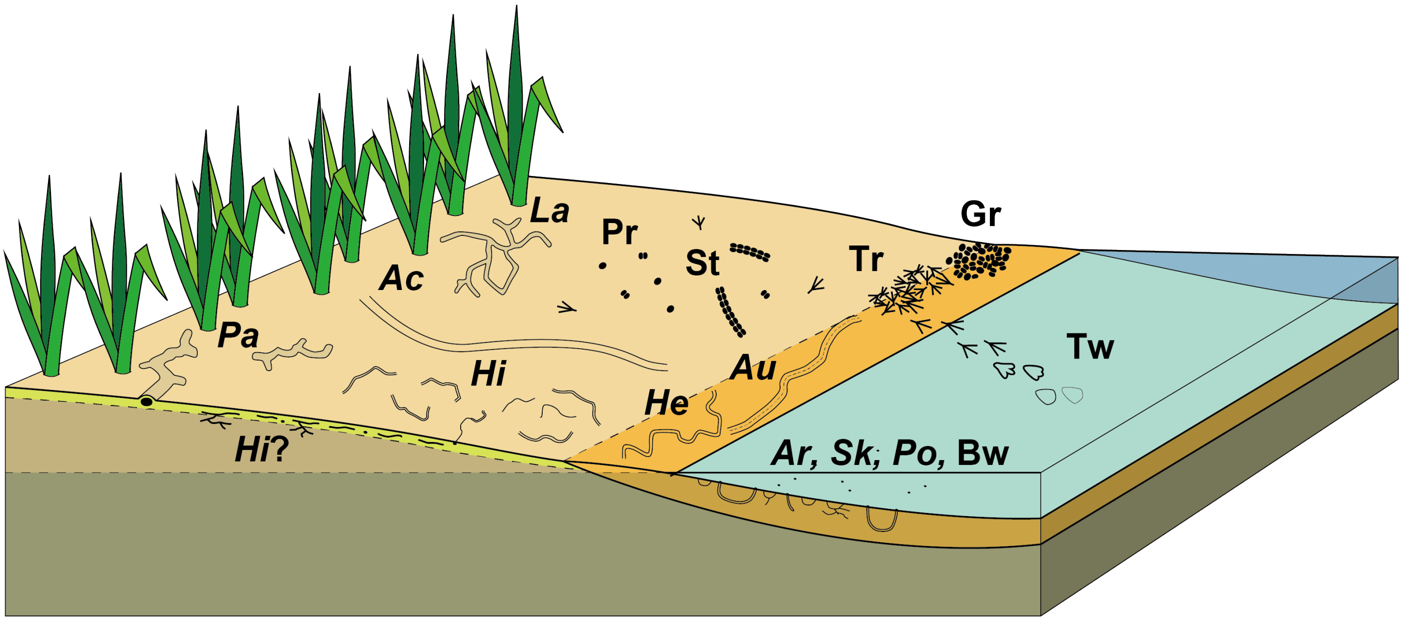

Figure 8 | Schematic representation of the distribution of animal traces that occur at Cooking Lake. Both incipient invertebrate traces (*Ac* = incipient *Archaeonassa*; *Ar* = incipient *Arenicolites*; *He* = incipient *Helminthopsis*; *Hi* = incipient *Helminthoidichnites*; *La* = incipient *Labyrintichnus*; *Pa* = incipient *Paracanthorhaphe*; *Po* = incipient *Polykladichnus*; *Sk* = incipient *Skolithos*; Bw = unassigned boxwork burrows) and vertebrate traces (Gr = Grazing; Pr = Probing; St = Stitching; Tr = Trampling; Tw = Trackway) are shown. The lake profile and sizes of the animal traces are not to scale.

trace assemblage distinct from other areas. The invertebrate ichnofauna found at this zone are comparable to those making up the *Mermia* Ichnofacies. However, it should be noted that the Morphotypes VI and VII reflect arthropod locomotion rather than grazing behaviour, warranting cautious ethological interpretation. Some trails of Morphotype IX grade into burrows of Morphotype III (incipient *Helminthoidichnites*), likely reflecting the tracemaker's response to increasing water saturation. In contrast, vertebrate trackways are characteristic of the *Scoyenia* Ichnofacies. Tracks formed in subaqueous environments are typically faint and susceptible to rapid destruction by wave action (see Figure 7A), clearly distinguishing between subaqueous and subaerial environments. The significance of this trace assemblage in the rock record is uncertain, as its location may fluctuate with changing lake levels and could be overlain by other traces over time.

In summary, there are major differences between the trace assemblages of the Cooking Lake and the archetypal continental ichnofacies. The subaqueous suites are dominated by penetrative burrows, whereas the subaerial suits have lower diversity, and less complex or large burrows compared to the archetypal *Scoyenia* Ichnofacies. However, when examining the behaviours responsible for these traces, there is a convergence with ichnofacies models where deposit feeding dominates the subaqueous suite and detritus feeding, dwelling, and locomotion are characteristic of the subaerial suite. The difference in the types of animal traces may be due to the differences in hydrology of high-latitude lakes compared to arid or semi-arid lakes, though further research on lakes similar to Cooking Lake is necessary to clarify this.

5.2. Invertebrate trace-tracemaker associations

Some of the traces at Cooking Lake were observed alongside their producers, thus allowing for direct associations between the trace with its tracemaker. Other tracemakers can be inferred from the fauna present at the lake site. A summary of all tracemakers is provided in Table 1. Of the nine invertebrate trace types observed, four were observed with the producer. Morphotype I (incipient *Skolithos* and *Arenicolites*) was found in association with chironomid larvae (Figure 4A). As previously discussed, chironomids construct U- or J-shaped burrows, as well as complex networks and meniscate back-filled forms (Chamberlain, 1975; McLachlan, 1977; Uchman & Álvaro, 2000; White & Miller, 2008). Linings are also observed, and in some cases, the entrance tubes may be elevated above the surface (McCall and Tevesz, 1982; Gingras et al., 2007).

Morphotype V (incipient *Paracanthorhaphe* or *Labyrintichnus*) was associated with larvae or adults of Heteroceridae (Figure 4H-I). These beetles produce meandering and branching burrows near the surface of muddy shores in fluvial and lacustrine environments (Chamberlain, 1975; Ratcliffe & Fagerstrom, 1980). The burrows, primarily used for feeding (Fodichnia), are created by both larvae and adults which feed on algae, plankton, and organic matter in the mud (Kaufmann & Stansly, 1979). The burrows observed at Cooking Lake were found within layers containing photosynthetic algae (Figure 4G). We also observed that the larvae tend to produce longer burrows compared to adults. This is likely because the adults can fly to new locations (Kaufmann & Stansly, 1979), whereas larvae remain in the burrow for extended periods. In this case, the burrow may also function as Domichnia.

Trails of Morphotype VI (incipient *Helminthopsis*) were observed being produced by an ant (Formicidae; Figure 5A). While *Helminthopsis* is generally considered a grazing trail, the trail observed here clearly represents Repichnia, where the ant likely landed accidentally on muddy sediment and attempted to free itself. Insect trails are typically classified as *Helminthopsis*, *Helminthoidichnites*, or *Gordia* depending on the degree of meandering and presence or absence of loops (Genise, 2017). Morphotype VI from Cooking Lake winds and meanders without self-overcrossing, hence it is identified here as incipient *Helminthopsis*. Given the accidental nature of the trails, their significance in the fossil record is likely minimal, but Metz (1987a) also recognized similar trails formed in ephemeral puddles and assigned them to *Helminthopsis*. The ichnogenus itself is not uncommon in lacustrine environments and has been reported by Buatois et al. (1996; 1997), Metz (2000), Kim et al. (2005), and Hu et al. (2014).

Trails of Morphotype VII (incipient *Aulichnites*), another example of Repichnia, were produced by Arctiidae caterpillars (Figure 5C). It is unclear whether the caterpillars were intentionally moving along the lake shores, perhaps in search of food and water, or if they accidentally ended up on the wet sediments. However, there were at least two independent trails observed, indicating that this behaviour is not uncommon. To the best of our knowledge, caterpillar trails have never been recorded in neoichnological studies. Nonetheless, Rowland & Caputo (2016) briefly mentioned in a field trip guidebook that *Paleohelcura* from aeolian sandstone may have been created by a caterpillar or scorpion. The caterpillar trail from Cooking Lake did not preserve the digit impressions, but instead it appeared as a bilobate trail with a faint median ridge. The weight of the caterpillar displaced the soft, silty sediments on the surface, producing distinct lateral ridges. Where median ridges are present, the morphology matches the description of *Aulichnites* in Buatois & Mángano (1993). Although the formation of *Aulichnites* is usually attributed to gastropods, some interpretations suggest they can also be made by crawling arthropods (Buatois & Mángano, 1993; Khaidem et al., 2015).

Morphotype II (incipient *Arenicolites*, *Polykladichnus*, and boxwork burrows) are much smaller than Morphotype I, and the chironomid larvae would not have been able to produce them. Although active construction was not observed, ostracods were found entering these burrows (Figure 4B), making them the most likely producers. Indeed, some ostracods are known to have an infaunal life mode (Tevesz & McCall, 1976; Starek et al., 2010; Decrouy et al., 2012), yet the architecture of their burrows remains unreported. Retrum et al. (2011) performed a lab-based neoichnological study on ostracods and identified various trails, resting traces, and U-shaped burrows. In addition, Chamberlain (1975) observed that some ostracods can leave small boxwork burrows consistent with Morphotype II from Cooking Lake. Another possible candidate for constructing Morphotype II are ceratopogonid larvae (Figure 3A), which have long and slender bodies that can fit inside the burrows. The larvae feed on algae, organic detritus, and other small invertebrates, and can be found burrowing in the substrate (Mullen & Hribar, 1988; Mullen & Murphree, 2019). Although the specific burrow morphologies of Ceratopogonidae larvae are unknown, Metz (1987b) observed that they are capable of producing *Cochlichnus*-like meandering trails along ponds and streams. Given the small size of these burrows and their formation in a soupy substrate, their preservation into the rock record is questionable. Nevertheless, Retrum et al. (2011) noted that either desiccation of clay immediately after trace emplacement or burial following non-erosive depositional processes could potentially preserve fine-scale traces left by small invertebrates like ostracods.

Burrows of Morphotypes III and IV, as well as trails of Morphotype IX (incipient *Helminthoidichnites*), share similarities in size and architecture, and sometimes grade from one form to another (Figure 4C), suggesting that the traces are probably produced by the same organism. The difference in form is likely influenced by the water table (cf. Hasiotis, 2002, 2007; Buatois & Mángano, 2007). At higher water tables, the tracemaker is restricted to the air-water interface, resulting in Morphotype III and Morphotype IX, while at lower water tables, they can dig deeper into the substrate, forming Morphotype IV. Potential insects responsible for producing these burrows at Cooking Lake include fly larvae from Ephydridae, Stratiomyidae, and Tipulidae (Figure 3B-E). Dipteran larvae, such as the species found at Cooking Lake, are known to produce simple burrows similar to those observed, although some may exhibit branching and/or backfills (e.g., Ahlbrandt et al., 1978; Mángano et al., 1996; Uchman, 2005; Muñiz Guinea et al., 2014; Sanz-Montero et al., 2013; Scott et al., 2020). In the rock record, *Helminthoidichnites*, along with morphologically similar trace fossils such as *Helminthopsis* and *Gordia*, are relatively common in lacustrine deposits, and they are interpreted as grazing traces of insect larvae or nematomorphs (Metz, 2000; Melchor et al., 2006; Fillmore et al., 2017).

Morphotype VIII (incipient *Archaeonassa*) consist of elongated furrows with well-defined lateral ridges that are similar to Morphotype VII but are slightly smaller and lacking a median ridge. Although it is possible that the trails were produced by caterpillars, as with Morphotype VII, they may also be made by field slugs (Agriolimacidae; Figure 3F) which were common near vegetation along the shore. Although no neoichnological experiments specifically related to slugs have been conducted, other gastropods are known to produce similar trails (cf. Melchor et al., 2003; Baucon, 2021). The well-developed lateral ridges and the complete absence of a median ridge in Morphotype VIII are morphologically comparable to *Archaeonassa*. According to Buckman (1994), *Archaeonassa* traces are epireliefs with two parallel ridges that delineate a central zone which can be flat, convex, or concave. *Archaeonassa* traces are found in lacustrine deposits and are usually interpreted as trails made by gastropods or arthropods (Genise et al., 2010; Sodré et al., 2023; Zouheir et al., 2023).

All of the burrows observed at Cooking Lake were open burrows, which would require passive filling with a contrasting lithology to be preserved and identified as trace fossils. Except for Morphotypes VII and VIII, all of the traces are relatively small and would only persist if they were rapidly buried by non-erosive depositional events. However, extremely small trace fossils (as small as 0.25 - 0.5 mm) have been found in lacustrine deposits in the past (e.g., Pollard & Hardy, 1991; Uchman et al., 2009). Neoichnological studies, such as this one, can provide valuable insights for interpreting ancient lake deposits.

5.3. Vertebrate trace-tracemakers and application to vertebrate ichnofacies

Vertebrate traces found along Cooking Lake include both walking (Repichnia) and foraging (Fodichnia) traces left by shorebirds. The incumbent anisodactyl (incipient *Koreanaornis*) and tetradactyl (incipient *Ardeipeda*) are unequivocally attributed to shorebirds (Figure 7B). Both fossil *Koreanaornis* and *Ardeipeda* tracks are often interpreted as shorebird traces (e.g., Lockley et al., 1992, 2021; Anfinson et al., 2009; Falk et al., 2014; de Valais & Cónsole-Gonella, 2019). The larger palmate trackways (incipient cf. *Presbyornithiformipes*; Figure 7A) can be produced by *Recurvirostra americana* or dabbling ducks, although other resident waterfowls, such as Canada goose: *Branta canadensis*, may also be responsible.

Probing traces occurred sporadically, in linear patterns, or clustered together, recording the feeding behaviour of the birds. Sporadic probings are produced when a bird moves while probing (Figure 6E), a behaviour observed in both modern and fossil records (e.g., Boettcher et al., 1994; Falk et al., 2010; Fiorillo et al., 2011; Abbassi et al., 2016; Melnyk et al., 2022; Zonneveld et al., in press-b) and noted in all of the shorebirds at Cooking Lake, except for *R. americana*. The aligned probing traces are most likely related to stitching behaviour, where the tracemaker continuously probes sideways without lifting its head from the substrate (Figure 6D) (Angarita-Báez & Carlos, 2023; Zonneveld et al., in press-b). Stitching was only observed in *Limnodromus scolopaceus*, although other species may also use this method. In some cases, the stitching traces followed invertebrate burrows, implying the bird was targeting the burrower (Figure 7D). Comparable grazing trace fossils have been found in Neogene red beds from Iran (Abbassi et al., 2016).

None of the behaviours observed at Cooking Lake can be attributed to the densely clustered probe marks (Figure 7E), though it is possible that these represent grazing traces on biofilms (cf. Elner et al., 2005; Mathot et al., 2010; Zonneveld et al., in press-b). Birds tend to walk slower during grazing than foraging (Kuwae et al., 2008), which could explain the high density of probe marks. According to Kuwae et al. (2012), smaller shore birds, especially sandpipers belonging to *Calidris* sp., are more likely to exhibit grazing behaviours. Although grazing behaviour has not been reported for *Calidris bairdii* or *Calidris himantopus* at Cooking Lake, it remains a possibility for these and related species at the lake site. Clustered probe marks indicative of potential grazing behaviour has also been reported from Eocene coastal plain deposits in Indonesia (Zonneveld et al., 2024).

Although the concept of vertebrate ichnofacies has received mixed reviews, there is mounting discussion about its validity and utility (e.g., Lockley et al., 1994; Hunt & Lucas, 2007, 2016; Santi & Nicosia, 2008; Melchor, 2015). According to Hunt & Lucas (2016), unlike invertebrate ichnofacies (“ethoichnofacies”), vertebrate ichnofacies (“biotaxonichnofacies”) are more concerned about distribution patterns of biotaxa, which can provide insights into evolution and ecology of vertebrates. However, this concept, is still in its infancy, and the usefulness of vertebrate ichnofacies remains questionable (Melchor, 2015). The question of whether vertebrate ichnofacies are valid requires a thorough examination of trace fossil assemblages from various localities, as well as a deeper exploration on the underlying philosophy – topics that are beyond the scope of this paper. Therefore, we will limit our discussion to a brief comparison of the trace assemblages with existing models.

The abundance of shorebird tracks at Cooking Lake fits the *Grallator* Ichnofacies (*Avipeda* ichnocoenose) as proposed by Hunt & Lucas (2016). The *Grallator* Ichnofacies represent a dominance of tridactyl or tetradactyl bipeds (birds and non-avian theropods) with subordinate occurrences of bipedal and quadrupedal tetrapods, such as ornithischians, sauropods, and herbivorous mammals, primarily found along lacustrine margins (Hunt & Lucas, 2007, 2016). Based on observations at Cooking Lake and fossil evidence from Cenozoic lake successions (e.g., Genise et al., 2009; Melchor et al., 2012; Kim et al., 2013), it may be beneficial to include the foraging traces as part of the *Avipeda* ichnocoenoses to better highlight the ecological niches occupied by these shorebirds.

6. Conclusions

Overall, the invertebrate traces found at Cooking Lake were simple and diminutive compared to the archetypal ichnofacies and those found in tropical or arid regions (cf. Hamer & Sheldon, 2010; Hasiotis et al., 2012). The primary invertebrate tracemakers were insects, particularly dipteran larvae, and except for slugs, no other macrobionts were observed during the study. While climate could partly explain this trend, the wet nature of these lake shores likely also contributed. It is interesting to note that the ethologies underpinning the traces at Cooking Lake are not very different from those represented in models for archetypal ichnofacies. However, there is a clear gap in our understanding of trace patterns in similar lake environments, underscoring the need for further research on additional intra-forest lakes.

One feature of forest lakes not addressed in this study is the impact of seasonality on trace assemblages. Lake temperatures can go up to 20°C in the summer, but in winter, the lakes become completely ice-covered (Mitchell & Prepas, 1990). The cold temperatures and anoxic conditions in winter may inhibit large animals from colonising the lake, potentially leading to different trace signatures. Additionally, because of this seasonality, the present findings are only a snapshot of invertebrate trace assemblages, and it might be necessary to conduct further studies at different seasons to fully understand the ichnology of lakes in a forested area. This is especially true for subaqueous settings where the water chemistry changes dramatically during the warm months (Mitchell & Prepas, 1990).

The high primary productivity and abundance of invertebrates at the lake site provide an excellent feeding ground for shorebirds, resulting in an abundance of their tracks and foraging traces at Cooking Lake. The vertebrate trace assemblages are comparable to the *Grallator* Ichnofacies. The sporadic probing and stitching behaviours observed are related to the exploitation of invertebrates, whereas clustered probe marks may indicate grazing behaviours. Foraging traces of shorebirds are generally understudied (Zonneveld et al., in press-b), and their spatial-temporal distribution in lakes is not well understood. Hence, the types and pattern of shorebird foraging traces at Cooking Lake serve as a valuable reference for future studies at different lakes.

The study of modern traces at Cooking Lake provides a foundation for understanding animal traces and trace fossils in high latitude lakes that occur within forests. However, further research is needed to explore the spatial variation in trace assemblages to deepen our understanding of the ichnology of forest lake systems. Given that Aspen Parkland is situated between the Boreal Forest and Grassland Prairies, comparing it with lakes in those two distinct ecosystems could help identify specific environmental factors that influence lake fauna and their traces. Additionally, given the diversity of lakes throughout high-latitude regions of North America, Europe, and Asia, a comparative study across different continents is possible. As previously mentioned, the lakes in higher latitudes are highly affected by seasonal changes, highlighting the need for further research on trace assemblages during different seasons. Identifying the seasonal variations may enhance our interpretation of trace fossils from lacustrine successions by helping to determine whether shifts in trace fossil assemblages are due to seasonal fluctuations or a change in the depositional environment.

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Author contribution

The authors confirm contributions as follows: Conceptualization: R. Kimitsuki, J.-P. Zonneveld, and M. Gingras; Investigation: R. Kimitsuki, B. Coutret, K. Rozanitis, and Y. Li; Supervision: J.-P. Zonneveld, K. Konhauser, and M. Gingras; Funding acquisition: J.-P. Zonneveld, and M. Gingras; Original draft preparation and visualization: R. Kimitsuki. All other authors reviewed and edited the original manuscript.

Data availability

The authors confirm that data associated with the interpretations made herein are presented within the article.

Conflict of interest

We have no conflict of interest to disclose.

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