



Integrated Ichnofacies models for deserts: Recurrent patterns and megatrends



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ABSTRACT

Although it is commonly assumed that the trace-fossil record of eolian dunes and associated environments is invariably poor, a systematic review of the available information indicates that this is not necessarily the case. A model involving five main phases of colonization of desert environments through the Phanerozoic is proposed in this paper. The first phase (Cambrian–Silurian) involved animal incursions into coastal dune fields directly from the sea, although it is unlikely that these animals would have remained for long periods of time in coastal deserts. The second phase (Devonian) reflects the activities of dune pioneers that left their fluvial habitat to enter temporary or permanently into inland deserts. The third phase (Carboniferous–Permian) involved the colonization of deserts by tetrapods. The fourth phase (Triassic–Cretaceous) involved a major exploitation of the in-faunal ecospace as reflected by the appearance of more varied behavioral patterns in sub-superficial structures. The fifth phase (Paleogene–Recent) reflects the appearance of the ecological dynamic that characterizes modern desert communities. The invertebrate ichnofacies for eolian dunes is re-named herein as the “*Octopodichnus*–*Entradichnus* Ichnofacies” honoring the seminal work of previous workers who simultaneously tackled the issue of eolian dune ichnofacies. The *Chelichnus* ichnofacies is retained for vertebrate trace-fossil assemblages in eolian settings. Both ichnofacies occur in mobile and temporary stabilized sandy substrates, subject to frequent erosion and deposition, and to strong seasonality. Desert settings consist of complex mosaics of habitats or physical units associated with organism activity. Trace-fossil distribution can be understood as reflecting the partitioning of desert settings in a mosaic of landscape units, characterized by water content and its temporal fluctuations, nutrient availability, nature of the substrate, and the dominant organisms present. In turn, desert systems are dynamic entities that change as a response to regional climate. Landscape units, such as eolian sand seas, salt flat and playa lake systems, ephemeral rivers and alluvial fans, interact in response to regional-scale climate variations in hyper-arid, arid, and semiarid climatic settings. Ancient deserts completely developed under hyper-arid climatic conditions rarely preserve trace fossils due to the absence of moisture near the surface. However, the alternation of wet periods may represent windows for life development and thus, preservation of biogenic structures. Arid deserts display complex patterns of dunes combined with dry, wet, and flooded interdunes. Dry desert elements (e.g. dunes, interdunes, sand sheets) typically record the *Entradichnus*–*Octopodichnus* and *Chelichnus* Ichnofacies. Slight rises in regional precipitation produce elevation of the water table and increase of fluvial discharges that provide water and sediment to the system. These processes may result in the local concentration of trace fossils in wet interdunes and ephemeral fluvial systems, illustrating the *Scoyenia* and *Chelichnus* Ichnofacies. In semiarid systems playa lakes expand by the addition of freshwater, evolving into freshwater lakes, and fluvial systems may become more common; lake margins and fluvial overbanks typically contain trace-fossil assemblages that may be ascribed to the *Scoyenia* Ichnofacies.

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1. Introduction

It is commonly mistakenly assumed that deserts have low biotic diversity as well as biomass. Accordingly, it is usually thought that the trace-fossil record of desert eolian dunes is invariably poor. However, a review of the available data indicates that the documentation of trace fossils in desert eolian dunes and coastal eolian dunes present in arid climates is more extensive than currently assumed (e.g. Ahlbrandt et al., 1978; Alonso-Zarza et al., 2008; Braddy, 1995; Brady, 1947, 1961; Brand, 1979; Brand and Tang, 1991; Carvalho, 2009; Curran and White, 1991; Ekdale and Bromley, 2012; Ekdale and Picard, 1985; Fornós et al., 2002; Gilmore, 1926, 1927, 1928; Hanley et al., 1971; Lockley et al., 1998; Loope, 1984; Loope et al., 1998; McKee, 1934, 1947; McKeever, 1994; McKeever, 1991; Melchor, 2001; Sadler, 1993). Ancient desert systems are well understood from a sedimentologic perspective and these depositional settings are well documented in the rock record throughout the Phanerozoic (Blakey et al., 1988; Mountney, 2004, 2006; Rodríguez-López et al., 2014). The ichnology of eolian dunes, particularly its potential for ichnofacies recognition, has experienced renewed interest during the last ten years with the simultaneous publication of two seminal papers (Ekdale et al., 2007; Hunt and Lucas, 2007a) and a more recent review on eolian ichnology (Ekdale and Bromley, 2012). Despite these major efforts, an integrated ichnofacies model, including both invertebrate and vertebrate traces, which accounts for the impact of macroevolutionary changes in trace-fossil composition, has not yet been proposed and discrepancies about which are the recurrent characteristics of eolian ichnofaunas through time still persist. Understanding the common traits of eolian ichnofaunas and their changing nature through the Phanerozoic as a result of macroevolutionary breakthroughs is a challenging task. Herein we present a review of the current state-of-the-science of desert ichnology, and further use our analysis to propose a rationalization and reorganization of the current models, terminology and definitions attending their ecological and evolutionary constrains. The aims of this paper are as follows: (1) to develop an ichnofacies model that accounts for an integrated analysis of vertebrate, invertebrate, and plant ichnologic data from desertic environments; (2) to generate a model that accounts for a variety of related sub-environments within deserts involving not only eolian dunes, interdunes, and sand sheets but also other alluvial and lacustrine depositional settings that interact at a regional scale; (3) to analyze the paleoecology of the tracemakers; and (4) to provide a macroevolutionary framework to explain the ichnologic data.

2. Background

The primary conceptual framework in which the environmental significance of ichnologic data is analyzed in this paper is the ichnofacies model. Twenty years ago our understanding of continental ichnofacies lagged remarkably behind our knowledge of marine ichnofacies, although this situation has significantly changed due to a marked increase in the pace of research (e.g. Buatois and Mángano, 1995, 2004, 2009; Ekdale et al., 2007; Genise et al., 2000, 2010; Hunt and Lucas, 2007a; Smith et al., 1993). In addition, there have recently been renewed attempts to evaluate the role of macroevolutionary controls on ichnofacies composition for both terrestrial and freshwater settings (Buatois and Mángano, 1993; Buatois et al., 1998; Genise and Bown, 1994; Genise et al., in press; Miller and Labandeira, 2002).

2.1. Continental ichnofacies

Originally, Seilacher (1963, 1967) recognized only one ichnofacies for continental environments, the *Scoyenia* Ichnofacies. As noted by (Frey et al. (1984), for some time, this ichnofacies was used uncritically as a synonym for any association of trace fossils in continental environments. Subsequently, a series of attempts to restrict its usage or to subdivide it has been presented. Frey et al. (1984) proposed to restrict the use of the *Scoyenia* Ichnofacies for continental trace-fossil associations dominated by meniscate structures that occur either in subaqueous freshwater deposits that are episodically exposed or terrestrial deposits episodically submerged. On the basis that arthropod trace fossils are an important component in the original definition of Seilacher (1963) and that many ichnocoenoses in similar environmental conditions are dominated by arthropod trackways, Buatois and Mángano (1995) expanded the definition of the *Scoyenia* Ichnofacies to accommodate arthropod trackways. Smith et al. (1993) proposed the *Termitichnus* association as a subdivision of the *Scoyenia* Ichnofacies that includes terrestrial trace fossils. However, Buatois and Mángano (1995) considered this association of the same hierarchy as the *Scoyenia* Ichnofacies. In turn, these authors postulated a third archetypal ichnofacies, the *Mermia* Ichnofacies for permanently subaqueous lacustrine environments. Accordingly, Buatois and Mángano (1995) presented a model of three ichnofacies at the same hierarchical level: the *Termitichnus*, *Scoyenia* and *Mermia* Ichnofacies. Subsequently, Genise et al. (2000) defined an ichnofacies for paleosols of herbaceous communities, the *Coprinisphaera* Ichnofacies. These authors also suggested that the paleoecologic and paleoenvironmental implications of the *Termitichnus* Ichnofacies are

very general, favoring a research program aimed to the establishment of a series of ichnofacies for paleosols developed under a spectrum of climatic conditions. This program gradually moved forward during the last decade, following an increased understanding of the wide variety of biogenic structures and producers in paleosol settings (Düringer et al., 2006; Genise, 2004; Krause et al., 2008; Laza, 2006; Verde et al., 2007), leading to the establishment of a new paleosol ichnofacies for carbonate-rich paleosols, the *Celliforma* Ichnofacies (Genise et al., 2010).

Lockley et al. (1994) first applied the ichnofacies concept to associations of vertebrate trace fossils. The delay in the proposal of a model for vertebrate traces is, most likely, because vertebrate and invertebrate ichnology have mostly been developed as two separate disciplines. This is related, to a large extent, to the morphological and behavioral differences of the producers, the nature of their environments of preservation, and the difficulty of treating them as a single object of analysis. Although the tetrapod ichnofacies model has been the focus of much debate and has met with limited acceptance, some ideas are highly valuable and have contributed to a fruitful exchange of opinions among ichnologists (Bromley, 1996; Conti et al., 2007; Keighley and Pickerill, 2003; Lockley, 2007; Santi and Nicosia, 2008). For example, in the case of the *Chelichnus* Ichnofacies developed for eolian settings, far from being an environmental or morphological artifact, it seems to capture the archetypal tetrapod communities of deserts.

2.2. Eolian ichnofacies

Two ichnofacies for eolian environments, the *Laoporus* and the *Brasilichnium* Ichnofacies, were proposed in the original model of vertebrate ichnofacies by Lockley et al. (1994). The *Laoporus* Ichnofacies emphasizes the presence of synapsids in early Permian eolian assemblages. Later, the assemblage was renamed as the *Chelichnus* Ichnofacies to account for the synonymy of the two ichnogenera (*Chelichnus* and *Laoporus*) (Hunt and Lucas, 2005, 2006; Lockley et al., 1995; Mckeever and Haubold, 1996; Morales and Haubold, 1995). The *Brasilichnium* Ichnofacies is similar to the *Chelichnus* Ichnofacies, including also the presence of synapsid tracks, but during a different time span, Late Triassic–Early Jurassic.

Subsequently, Hunt and Lucas (2007a) redefined the *Chelichnus* Ichnofacies and proposed the new *Octopodichnus* Ichnofacies. These authors considered the *Chelichnus* Ichnofacies for tetrapod associations of low diversity, characterized by ichnotaxa with short digits and similar *manus* and *pes* impressions, thus including the ichnogenera *Chelichnus* and *Brasilichnium* (Fig. 1). This ichnofacies is recurrent in dune facies of eolian environments from the early Permian to the Early Jurassic. Hunt and Lucas (2007a) also considered that other tetrapod ichnofacies could be present in eolian environments. For example, the *Grallator* Ichnofacies, which also occurs in lacustrine facies associated with eolian settings. The *Octopodichnus* Ichnofacies was defined by Hunt and Lucas (2007a) for eolian dune trace-fossil associations that include a low diversity of arthropod locomotion traces, mainly spiders and scorpions (e.g., *Octopodichnus*, *Paleohelcura*) (Fig. 1). Simultaneously, Ekdale et al. (2007) defined the *Entradichnus* Ichnofacies for trace-fossil

associations of mostly non-vegetated eolian dune fields, consisting of simple shallow vertical (e.g., *Skolithos*, *Arenicolites*, *Digitichnus*) and horizontal (e.g., *Palaeophycus*, *Planolites*) burrows, in addition to meniscate trace fossils (e.g., *Entradichnus*, *Taenidium*) produced by arthropods (Fig. 1). This ichnofacies is temporally broader than the *Chelichnus* and *Octopodichnus* Ichnofacies, it ranges from the Permian to the Holocene. The *Entradichnus* Ichnofacies is mostly based on the study of Jurassic examples, more specifically those from the Navajo Sandstone of Utah. Conversely, Hunt and Lucas (2007a) based the *Chelichnus* and *Octopodichnus* ichnofacies essentially on Permian ichnoassemblages, as recognized in the classic Coconino Sandstone of Arizona. The diverging characterization of these ichnofacies undoubtedly resulted from the use of disparate databases (Buatois and Mángano, 2011).

In the last years, numerous authors highlighted the concurrent characteristics of the eolian trace-fossil assemblages in the known contrasting *Chelichnus*, *Octopodichnus*, and *Entradichnus* ichnofacies and suggested the integration of these separate models (e.g. Buatois and Mángano, 2011; Ekdale and Bromley, 2012; Krapovickas et al., 2010, 2015). Originally, Hunt and Lucas (2007a) emphasized the close correspondence between the *Octopodichnus* and *Chelichnus* Ichnofacies (Hunt and Lucas, 2007a, p. 67). This same idea was already stated by Lockley et al. (1994) in the original definition of the *Chelichnus* Ichnofacies where the authors indicated the common correspondence between *Laoporus* (= *Chelichnus*) and invertebrate trace fossils, such as *Octopodichnus* and *Paleohelcura*. Subsequently, Buatois and Mángano (2011) integrated the available invertebrate eolian ichnofacies models into the *Octopodichnus*–*Entradichnus* Ichnofacies. These authors explained the compositional changes between the *Octopodichnus* and *Entradichnus* associations as related to the radiation of new arthropod producers during the Mesozoic (see also Buatois et al., 1998, fig. 5). Finally, Ekdale and Bromley (2012) proposed that the *Octopodichnus* and *Chelichnus* Ichnofacies of Hunt and Lucas (2007a) should be subsumed within the *Entradichnus* Ichnofacies, but the rationale behind this decision was not fully developed. In our view, all these elements are key parts of integrated archetypal model, in which the differences between associations could mostly correspond to compositional or evolutionary turnovers within desert communities.

3. Desert ichnofaunas in deep time

The ichnology of eolian deposits can be broadly categorized into two groups: assemblages representative of inland sand seas, corresponding to ample expanses of high sand dunes with little or no vegetative cover (e.g. Ahlbrandt et al., 1978; Ekdale and Picard, 1985; Gilmore, 1926, 1927, 1928; Mckeever, 1994; Sadler, 1993), and assemblages from desert coastal eolian settings where dunes are generally paralleling marine shorelines, usually vegetated, and typically associated with beaches and tidal flats (e.g. Draganits et al., 2001; Phelps, 2002; Trewin and McNamara, 1994). Even though the latter ichnoassemblages are essentially fully terrestrial, they may include traces produced by marginal-marine faunas.

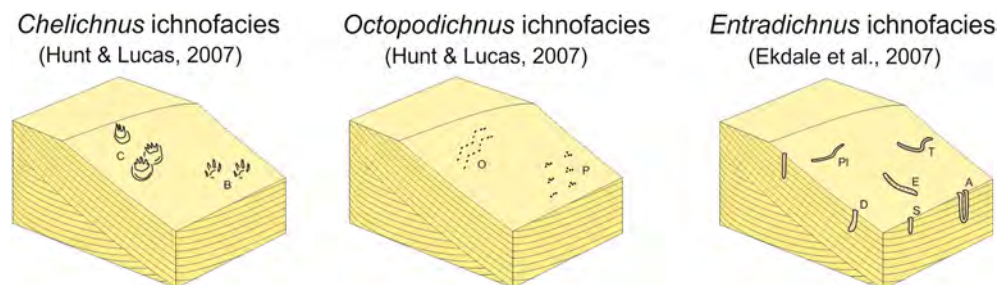


Fig. 1. Eolian ichnofacies models proposed by Hunt and Lucas (2007a), and Ekdale et al. (2007). A: *Arenicolites*, B: *Brasilichnium*, C: *Chelichnus*, D: *Digitichnus*, E: *Entradichnus*, O: *Octopodichnus*, P: *Paleohelcura*, Pl: *Planolites*, S: *Skolithos*, T: *Taenidium*.

3.1. Paleozoic

Lower Paleozoic ichnoassemblages from eolian environments are unusually reported and the continental nature of several lower Paleozoic ichnofaunas has been questioned (Buatois et al., 1998; Minter et al., 2016a,b). One of the most relevant examples is recorded from the Nepean Formation of Ontario (Canada), in a Furongian (late Cambrian) to Early Ordovician coastal-dune succession (MacNaughton et al., 2002). It represents animal incursions into land, and involves large trackways produced by amphibious arthropods (euthycarcinoids) during excursions out of the sea (Fig. 2a–d) (Braddy, 2004; MacNaughton et al., 2002). In more recent studies, the earliest record of incursions into deserts has been pushed backwards, by the finding of trackways (*Diplichnites* and *Protichnites*) produced by arthropods on coastal eolian dune deposits of the middle Cambrian Potsdam Group of northern New York (USA) (Hagadorn et al., 2011).

The Tumblagooda Sandstone of Western Australia records a diverse ichnofauna in mixed fluvial systems, with eolian dunes, waterlain sandsheets, flooded interdune, and deflation hollows (McNamara, 2014; Trewin and McNamara, 1994). The assemblage is regarded as early to middle Silurian in age (McNamara, 2014). Subaerial arthropod trackways such as *Diplichnites*, *Paleohelcura* and *Protichnites* occur in eolian dune deposits and represent, together with the above mentioned examples, some of the earliest reported trackways in eolian settings (Trewin and McNamara, 1994).

The actual invasion by animals of continental lands took place by the Silurian–Devonian transition and continued through the late Paleozoic

(Buatois et al., 1998; Labandeira, 2005; Minter et al., 2016b). By this time, a mobile arthropod epifauna was established in coastal-marine to alluvial-plain settings (Buatois et al., 1998). Late Silurian to Early Devonian fluvial-marine and terrestrial-marine transitional environments record subaerial arthropod trackways in small coastal dunes preserved in the middle to upper Silurian Tumblagooda Sandstone of Western Australia, the Lower Devonian Muth Formation of northern India, and the Devonian Taylor Group in the Darwin Glacier area of Antarctica (Draganits et al., 2001; Gevers et al., 1971; Hocking, 1991; Trewin and McNamara, 1994; McNamara, 2014). The subaerial trackways mostly correspond to *Palmichnium* and *Diplichnites* formed on the foresets of eolian dunes. These arthropod trackways mainly represent the activity of aquatic organisms that performed short excursions out of their marginal-marine habitats into coastal-eolian dunes. In the case of the Muth Formation, the trackways are interpreted as produced by stylonurid eurypterids migrating across the shoreline and climbing up slip faces of barrier island dunes (Draganits et al., 2001). The Tumblagooda ichnofauna consists of *Diplichnites*, most likely produced by arthropods, euthycarcinoids, and/or eurypterids on waterlain sand and eolian dunes of coastal fluvial out-wash (Hocking, 1991; Trewin and McNamara, 1994; McNamara, 2014). The environmental setting of the Taylor Group ichnofauna is still unresolved. Gevers et al. (1971) interpreted the outcrops as marine, while others favored a non-marine setting, including fluvial, estuarine, littoral, and eolian facies (Woolfe, 1990, 1993). Even though the ichnoassemblage is similar to that of the Muth Formation, no trackway was recorded on clear subaerially exposed facies (Draganits et al., 2001). Ultimately, the



Fig. 2. Trace fossils from the upper Cambrian–Lower Ordovician Nepean Formation of Ontario (Canada) (see MacNaughton et al., 2002). a: Trackway-bearing locality recording a coastal dune environment. Note well-exposed, large-scale foresets on the right. b: Quarried slab showing well developed adherence ripples. Lens cap for scale. c: *Protichnites* from the Kingston trackway site. d: Close-up of *Diplichnites*. Note the “back-push” mounds as good evidence for subaerial production by an animal going uphill. Compass is 10 cm long. Photographs courtesy of Rob MacNaughton.

emplacement of these arthropod trackways in eolian coastal dunes mostly represents littoral assemblages rather than fully terrestrial assemblages adapted for a subaerial life in sand dunes.

The first steps in the colonization of deserts occurred by the Middle Devonian. This early record is mostly represented by a low-diversity ichnofauna with superficial locomotion traces and sub-superficial dwelling and feeding traces. The earliest uncontroversial evidence of colonization of an erg system is from the Old Red Sandstone (Middle Devonian, Caherbla Group) of the southern British Isles (Ireland) (Morrissey et al., 2012). The ichnocoenosis is composed of arthropod trackways (*Palmichnium* and *Diplichnites*), meniscate burrows (*Entradichnus*), and simple horizontal and vertical burrows (*Palaeophycus*, *Cylindricum*, *Pustulichnus*) on dune lee-slopes. The most commonly preserved elements are *Palmichnium*, *Entradichnus* and *Palaeophycus* (Morrissey et al., 2012). This ichnofauna represents the activity of dune pioneers in excursions out of their fluvial habitat possibly to forage for detritus. *Palmichnium* is attributed to the activity of large stylonurid eurypterids, and *Diplichnites* is interpreted as produced by earthropleurids. Other sub-superficial traces are interpreted as produced by arthropods moving under the sand surface (Morrissey et al., 2012).

For examples from the Pennsylvanian to the Permian, eolian systems are largely documented from central-western North America (Blakey et al., 1988; Jordan and Mountney, 2010; Loope and Haverland, 1988; Loope, 1985; Peterson, 1988; Rodríguez-López et al., 2014). They mostly correspond to coastal deserts and constitute some of the major eolian deposit of North America, together with others that extended until Jurassic times (e.g. Blakey et al., 1988). The Middle Pennsylvanian Hermosa Group (Paradox Basin) and the lower Permian lower Cutler beds of central-western United States record large-diameter rhizoliths and meniscate burrows on flat erosional surfaces at the top of eolian sandstone bodies (Loope and Haverland, 1988; Loope, 1985, 2008). The flat surfaces correspond to eolian deflation to the water table level and the colonization of plants and invertebrates took place after deflation of the dunes when the sea level was relatively low (Loope, 1985, 1988). Recently, trace fossils have been recorded on dune slipfaces of the Pennsylvanian–Permian Weber Sandstone of Utah and Colorado, USA (Chure et al., 2014a). They correspond to unidentified tetrapod trackways possibly assigned to *Chelichnus*, arachnid trackways such as *Octopodichnus*, large horizontal burrows, and one trail of cf. *Diplichnites* (Chure et al., 2014a). By the early Permian, the trace-fossil record of eolian environments is copious, and assemblages are widespread mainly in North America and Europe. Classical ichnoassemblages are those from the Coconino Sandstone of Arizona (Gilmore, 1927, 1926, 1928) and the Corncockle, Locharbriggs, and Hopeman sandstones of Scotland (Duncan, 1831; Mckeever and Haubold, 1996; Mckeever, 1991). Eolian ichnoassemblages are also recorded in the Permian DeChelly Sandstone of Arizona (Fig. 3a–b), the Lyons Sandstone of Colorado, the Cedar Mesa

Sandstone of Utah, the Casper Sandstone of Wyoming and Colorado and the Cornberg Sandstein of Germany (Hanley et al., 1971; Lockley and Hunt, 1995; Lockley and Madsen, 1993; Lockley et al., 1998; Loope, 1984; Mckeever and Haubold, 1996; Mckeever, 1994). Conversely, Permian eolian ichnoassemblages are fairly scarce in Gondwana and, at present, are only recorded from lower Permian deposits of Argentina, namely the Patuquía and Yacimiento los Reyunos formations (Fig. 4a–c) (Krapovickas, 2010; Krapovickas et al., 2015).

The outstanding similarities among all Permian ichnofaunas suggest the establishment of global desert communities by that time. Arthropod locomotion trace fossils are widespread in sand-dune, dry-interdune, and sand-sheet deposits (Braddy, 1995; Brady, 1947, 1961; Krapovickas et al., 2010; Lockley and Hunt, 1995; Sadler, 1993). The most prevalent examples are *Paleohelcura* and *Octopodichnus*, and to a lesser extent, *Diplopodichnus* and *Cruziana* (Fig. 5a–d). The most commonly recorded ichnogenera, as *Octopodichnus* and *Paleohelcura*, have been interpreted as produced by spiders (Araneae) and scorpions (Scorpionida), respectively (Brady, 1947). The sub-superficial activity of arthropods is also widespread; they are recorded by simple vertical (*Skolithos*) and horizontal to subhorizontal (*Palaeophycus*) dwelling burrows, and meniscate (*Taenidium*) and simple (*Planolites*) feeding traces (e.g. Clemmensen and Abrahamsen, 1983; Hanley et al., 1971) (Fig. 5d–f). Root trace fossils are also recorded in Permian coastal-dune and sand-sheet deposits (e.g. Loope, 1984), but not in inland sand seas. Kozur et al. (1994) documented the presence of *Paleohelcura* in playa-lake margins within deserts from the lower Permian Michelbach Formation of Germany, extending its environmental range to playa lakes. In contrast to invertebrate trace fossils, which are relatively diverse, tetrapod footprints in dune, dry-interdune, and sand-sheet deposits are very similar morphologically and express a very low taxonomical diversity. The ichnogenus *Chelichnus* (= *Laoporus*) is recorded in all desert ichnoassemblages with tetrapod footprints, and it is almost invariably the only ichnotaxa present (Fig. 6a–e). It constitutes a well-defined morphotype; the footprints not only denote autopodia of high similitude, but also all trackways reflect comparable locomotion patterns that involve the presence of closely related taxa in deserts worldwide. Different speculations have been made regarding the *Chelichnus* producer (e.g. Haubold, 1971; Jardine, 1950; Mckeever, 1994). Original interpretations considered *Chelichnus* as produced by turtles (e.g. Jardine, 1950). From the 1970s to the 1990s a number of proposed producers emerged for *Chelichnus*, mainly pointing to an affinity with “pelycosaurs”, with the suggestion of caseid synapsids, basal synapsids, and non-therapsid synapsids as possible producers (e.g. Haubold, 1971, 1980, 2000; Mckeever, 1994). The wide temporal occurrence of *Chelichnus* during most of the Permian favored also the proposal of other trackmakers, such as pareiasaurs and anomodont therapsids (Mckeever, 1994). The most recent analysis of



Fig. 3. Permian DeChelly Sandstone at Jemez Mountains New Mexico, USA. a: General view of the outcrops. b: Detail of stacked cross-bedded eolian dune sets and cosets. The scale bar is 60 cm.



Fig. 4. Lower Permian Yacimiento Los Reyunos Formation at San Rafael, Argentina. a: General view of the outcrops. b: Detail of a dune foreset tracked surface. c: Cross strata sets truncated by bedform migration delineated by an erosional bounding surface. Scale segments = 1 cm.

Chelichnus interpreted them as produced by basal therapsids (Krapovickas et al., 2015). Additionally, footprints putatively produced by lacertids (e.g., *Stenichnus*, *Dromopus*) and undetermined tetrapods have been also recorded in the De Chelly, Cedar Mesa, and Cornberg sandstones (e.g. Haubold et al., 1995; Lockley and Hunt, 1995; Lockley et al., 1998; Loope, 1984).

The first evidence of underground behavior and burrowing by tetrapods in deserts are recorded in interdunes or dune bottomset deposits within sand-dune fields in the Permian Arran Basin of Scotland (Clemmensen and Abrahamsen, 1983).

3.2. Mesozoic

Desert trace fossils are scarce in early Mesozoic deposits. The late Permian–Early Triassic ichnoassemblages recorded in the Tumlin Sandstone of Poland (Fig. 7a–c) are preserved in wet and damp interdunes within deserts (Gradziński and Uchman, 1994; Ptaszyński and Niedźwiedzki, 2004). The invertebrate trace fossils mostly correspond to subaqueous trails and burrows made on temporary flooded settings, consisting of delicate simple (*Skolithos*) and U-shaped (*Arenicolites*) vertical burrows, bilobate trails (*Cruziana*), simple trails (*Gordia*), and meniscate structures (*Taenidium*) (Gradziński and Uchman, 1994). Vertebrate trace fossils include examples of those produced by animals with a life cycle closely related to the water, such as amphibians (*Batrachichnus*, *Limnopus*, and *Amphisauropus*) and others attributed to reptilians, including *Rhynchosauroides*, *Varanopus*, *Dimetropus*, *Chelichnus*, *Palmichnus*, *Paradoxichnium*, and *Phalangichnus* (Ptaszyński and Niedźwiedzki, 2004). In wet-damp interdunes, the local concentration of trackways, trails, and burrows is favored and, moreover, the preservation potential of biogenic structures is enhanced (Buatois and Mángano, 2011). The Tumlin assemblage is not similar to classical desert faunas, and most likely corresponds to an example of the *Scoyenia* Ichnofacies in wet interdunes related to

desert margins, where a tetrapod community mostly resembles that responsible of typical “redbed ichnoassemblages” of Hunt and Lucas (2006).

The Middle Triassic Helsby Sandstone Formation of the Cheshire Basin, UK comprises an unusual wet eolian system where accumulation was controlled by periodic fluvial flooding and oscillations of the water table occurring concurrent with dune migration (Mountney and Thompson, 2002). This contrasts with other wet eolian systems where typically the formation of bypass surfaces resulted as a consequence of the cessation of dune climbing due to interdune flooding events (Mountney and Thompson, 2002). Bioturbation mostly occurs in these episodically wetting and drying interdune surfaces and at other laterally adjacent locations of the Lower Keuper Sandstone and the Ormskirk Sandstone Formation (King and Thompson, 2000; Mountney and Thompson, 2002; Pollard, 1981). The tetrapod ichnofauna was mostly produced by archosaurs and diapsid reptiles, such as *Rhynchosauroides*, *Chirotherium*, *Dicynodontipus*, and other unidentified prints (Beasley, 1996; Benton et al., 1994; King and Thompson, 2000; Maidwell, 1915, 1914a, 1914b, 1911; Pollard, 1981). Invertebrate trace fossil associations were ascribed to the *Scoyenia* Ichnofacies by Pollard (1981) and characterized by arthropod trace fossils and meniscate burrows, namely *Rusophycus*, *Diplichnites*, *Planolites*, *Palaeophycus* and striated oblique burrows.

During the Late Triassic–Cretaceous, the number of eolian ichnoassemblages recorded in desert sand-sea deposits greatly increased. Classical examples, not only documenting invertebrate but also tetrapod trace fossils, are those of the Lower Jurassic Navajo Sandstone and the Middle Jurassic Entrada Sandstone of USA. In western USA the number of Upper Triassic to Lower Jurassic successions containing traces fossils preserved on desert settings is remarkable and include the Glen Canyon Group (the Wingate Sandstone/Moenave Formation, Kayenta Formation, and Navajo Sandstone), the Nugget Sandstone, and the Azteca Sandstone (Chure et al., 2014b; Ekdale and

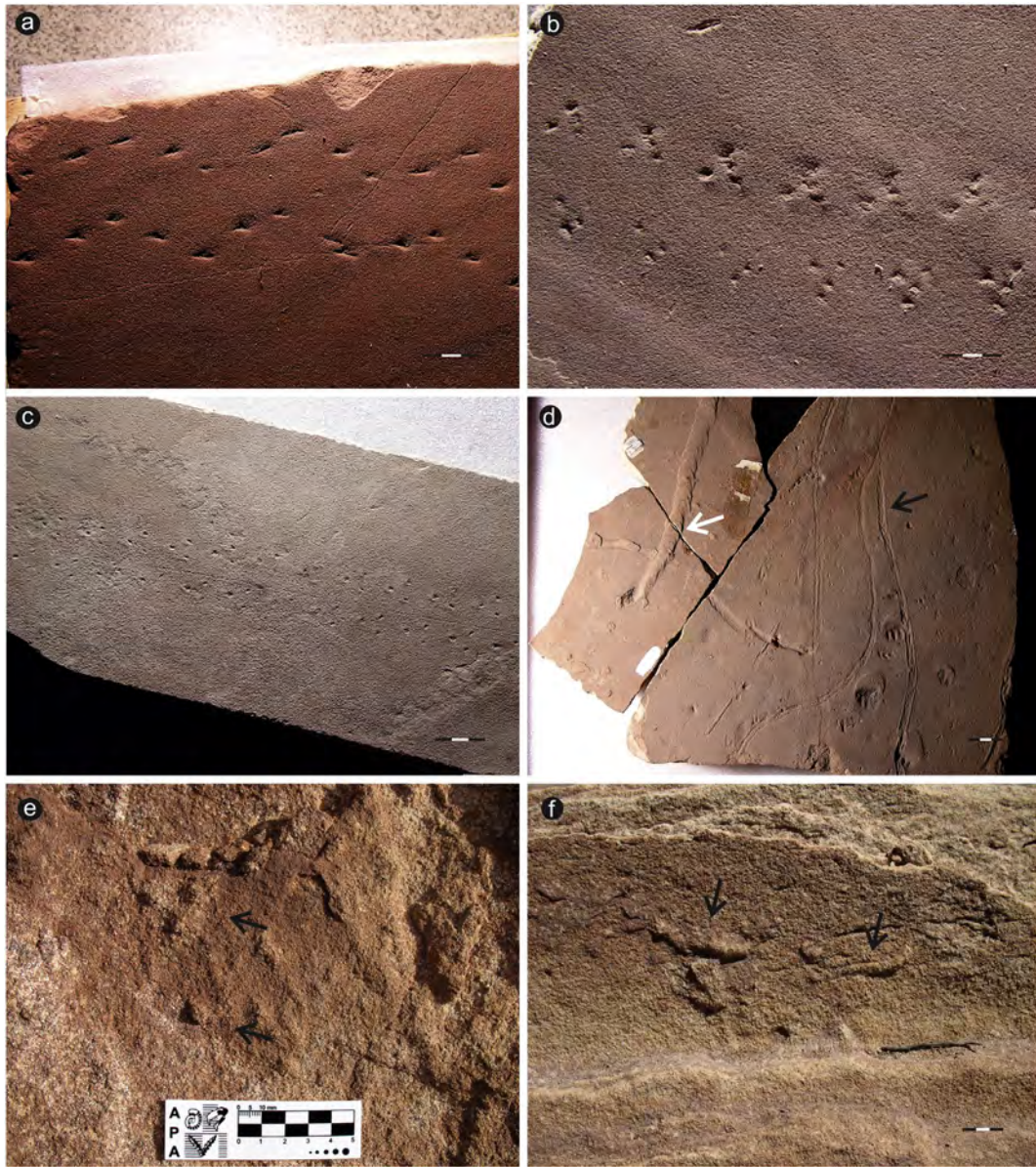


Fig. 5. Permian eolian invertebrate trace fossils. a–d: Specimens housed at the Museum of Northern Arizona, collected from the Coconino Sandstone (photographs courtesy of N. Minter). a: *Octopodichnus didactylus* (MNA N3679). b: *Octopodichnus raymondi* (MNA N3669). c: Holotype of *Paleohelcura 'dunbari'* (MNA N3660). d: Holotype of *Scolecocoprurus arizonensis* (white arrow) together with other traces included *Diplopodichnus* (black arrow) and *Chelichnus* (MNA N3655). e–f: Specimens from the Yacimiento los Reyunos Formation, Argentina. e. *Skolithos* isp. f. *Palaeophycus tubularis*. Scale segments = 1 cm.

Picard, 1985; Ekdale et al., 2007; Faul and Roberts, 1951; Good and Ekdale, 2014; Good, 2013; Hunt and Lucas, 2007b; Lockley and Hunt, 1995; Lockley et al., 2004; Milàn and Loope, 2007; Riese et al., 2011; Seiler and Chan, 2008; Tanner et al., 2006). In these deposits, subsurface invertebrate trace fossils are dominant and superficial arthropod trackways are almost absent. Typical ichnoassemblages are composed of dwelling burrows of horizontal (e.g., *Palaeophycus*, *Planolites*) and vertical to inclined (e.g. *Skolithos*, *Digitichnus*) orientation, as well as meniscate (e.g. *Taenidium*) and simple (*Planolites*) feeding trace fossils (Ekdale and Picard, 1985; Ekdale et al., 2007). Fossil root traces are recorded in eolian deposits of the Moenave Formation of Arizona and the Entrada Sandstone of Utah, where the moisture content in the sand dunes was enough to support a plant community (Loope, 2008, 2006a; Tanner et al., 2006). Large-sized excavations produced by therapsids are recorded in interdunes associated with rhizoliths and invertebrate trace fossils of the Navajo Sandstone of Utah (Riese et al., 2011) and crosscutting the foreset laminae of eolian dunes of the Nugget Sandstone of Utah (Engelmann et al., 2014), suggesting

that during the Mesozoic, underground burrows were numerous and fossoriality seems to be a strategy spread within tetrapods living in deserts. The diversity of tetrapod trackmakers in deserts increased significantly during the middle–late Mesozoic. Dominant elements are tridactyl footprints of non-avian theropods of multiple sizes, such as *Grallator*, *Anchisauripus*, *Eubrontes*, *Therangospodus*, and *Megalosauripus* (Fig. 8a–d) (Lockley et al., 2007, 1998; Lockley and Hunt, 1995; Loope, 2006b; Milàn and Loope, 2007; Rainforth and Lockley, 1996; Rowland et al., 2014; Seiler and Chan, 2008). Also, a characteristic ichnotaxon of Mesozoic deserts is *Brasilichnium* recorded in numerous localities (Fig. 9a–d). This ichnogenus was originally described from the Lower Cretaceous Botucatu Formation of Brazil and interpreted as small-sized mammal trackmakers (Leonardi, 1994). Later, it was also recognized in classical Lower Jurassic outcrops of USA, including the Nugget, Navajo, and Azteca sandstones, and the Moenave Formation, and reinterpreted as possibly produced by “therapsids” (Fig. 8e–f) (Chure et al., 2014b; Lockley and Hunt, 1995; Lockley et al., 1998; Loope, 2006b, 1988; Rainforth and Lockley, 1996; Rowland and



Fig. 6. Permian tetrapod track fossils: *Chelichnus*. a, e: Specimens housed at the University of California Museum of Paleontology collected from the Coconino Sandstone. a: UCMP 36851. e: UCMP 36867. Both materials originally described as “*Laoporus noblei*” (= *Chelichnus duncani*). b–d: Specimens housed at the Smithsonian Institution collected from the Coconino Sandstone. b: USNM 8422, holotype of “*L. noblei*” (= *C. duncani*). c: USNM 11146 holotype of “*Nanopus merriami*” (= *C. duncani*). d: USNM 11125 holotype of “*Dolichopodus tetradactylus*” (= *C. duncani*). Scale segments = 1 cm.

Mercadante, 2014). Other tetrapod footprints from aeolian deposits have been assigned to crocodylomorphs (*Batrachopus*), and prosauropod (*Otozoum*), sauropod (*Brontopodus*), and ornithischian (*Anomoepus*) dinosaurs of different sizes (e.g. Dentzien-Dias et al., 2007; Foster et al., 2000; Lockley and Hunt, 1995; Lockley et al., 1998; Loope, 2008, 2006a, 2006b; Milàn and Loope, 2007; Rainforth, 2001; Seiler and Chan, 2008).

Examples of ichnofaunas in desertic environments are also recorded from other localities worldwide. The Lower Jurassic Clarens Formation of Southern Africa is mostly composed of eolian dune deposits formed in a seasonally humid erg with local small ephemeral streams (Fig. 10a–b). It records vertical dwelling burrows (*Skolithos*), other enigmatic structures biologically induced, and dinosaur tracks (prosauropods/theropods). Additionally it preserves large horizontal cylindrical burrows produced by burrowing tetrapods in wet interdunes where the stability of the burrows was favored (Bordy and Catuneanu, 2002; Bordy, 2008; van Eeden and Keyser, 1971). Finally, the Clarence Formation records large free-standing sandstone pillars, interpreted originally as termitaria (see Bordy and Catuneanu, 2002). Alonso-Zarza et al. (2008) subsequently noted that plant roots and their associated

microorganisms could induce precipitation of carbonates around them creating structures much larger than the original roots, therefore reinterpreting these structures. Similar pillar-like structures have been originally described from Australia and named as megarrhizoliths (McNamara, 1995, 1986), and subsequently described in detail by Alonso-Zarza et al. (2008) for Pleistocene structures preserved on eolian deposits of Gran Canaria, Spain.

The Lower Cretaceous Djadokhta Formation of Mongolia is composed of mixed eolian–alluvial fan deposits. The beds contain dinosaur footprints in cross-section, small invertebrate dwelling burrows, and eolian-dune deposits that record invertebrate dwelling (*Skolithos* isp.) and feeding (*Planolites* isp. and *Entradichnus meniscus*) traces and root trace fossils. The latter would represent sparsely vegetated dunes during humid periods with more stabilized eolian bedforms (Loope et al., 1998; Seike et al., 2010). Detailed analysis by Seike et al. (2010) indicated that *E. meniscus* was characteristically oriented within eolian dunes (Fig. 11a–d). The trace fossils are parallel to the foreset lamina with most of the meniscate internal laminae of the burrow concave down-dips, possibly reflecting a producer behavioral response to dune architecture that has not been reported in modern dunes (Seike et al., 2010).

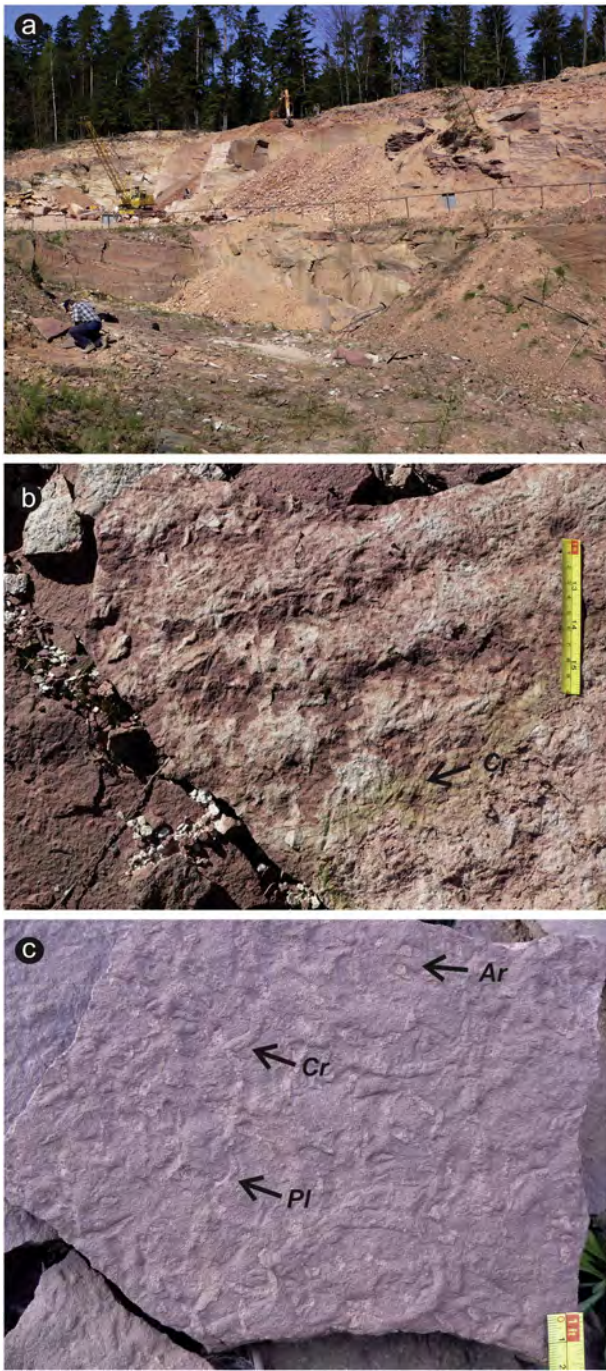


Fig. 7. Upper Permian–Lower Triassic Tumlin Sandstone of Poland (see Gradziński and Uchman, 1994). a: General view of trace fossil-bearing locality. b: General view of bioturbated surface, displaying discrete specimens of *Cruziana* (Cr). c: Close-up of bioturbated surface, showing *Cruziana* (Cr), *Arenicolites* (Ar) and *Planolites* (Pl). Photographs courtesy of Alfred Uchman.

The Lower Cretaceous Mulichinco Formation of western Argentina contains mixed fluvial and eolian deposits, encompassing a wide variety of subenvironments, such as eolian dunes, sand sheets, and interdunes (Zavala et al., 2005; Buatois, unpublished data). Eolian dune deposits contain vertical burrows, including *Arenicolites* (Fig. 12a) and *Skolithos* (Fig. 12a), together with horizontal burrows (*Palaeophycus*, Fig. 12a). Vertical burrows and mottled textures also occur in the sand sheet deposits (Fig. 12b–c). Associated sheet-like sandstones of fluvial origin are characterized by elements of the *Scoyenia* Ichnofacies, most notably *Taenidium* (Fig. 12d).

3.3. Cenozoic

Even though superficial arthropods are commonly observed in dunes of modern deserts, their fossil record is scarce, and in Cenozoic examples are almost absent. Because sand is a poor conductor of heat, the emplacement of arthropods at shallow depths provides temperatures suitable for survival for both hot and cold days (Crawford, 1988). Therefore, in recent deserts, active subsurface organisms are common in dune and interdune sands (Whitford, 2002). Accordingly, during the Cenozoic subsuperficial fossil burrows are a common element in dune deposits and in both dry and wet interdune deposits. Typical ichnofaunas of these environments include dwelling structures, such as *Palaeophycus*, *Skolithos*, *Gracilichnus*, and *Digitichnus*, but also feeding (*Taenidium* and *Planolites*) and hatching trace fossils (e.g. Ahlbrandt et al., 1978; Curran and White, 1991; Fornós et al., 2002; Melchor et al., 2015; Phelps, 2002; Smith and Mason, 1998). Nesting structures are also present in desert soils, including those of *Daimoniobarax nephroides* that closely resemble that of seed-harvesting ants (Smith et al., 2011).

In modern deserts, open burrows made in dunes and interdunes are produced by arthropods, including ants, lion ants, scorpions, spiders, solifuges, crickets, beetles, and centipedes (Fig. 13) (Phelps, 2002 and references therein). In order to produce open burrows in eolian environments, usually arthropods build structures in sands that are wet, well compacted or supported by vegetation (Buatois and Mángano, 2011; Phelps, 2002; Whitford, 2002). According to Cloudsley-Thompson (1991), a few arthropods, such as lion ants and some spiders, construct permanent excavations in non-stabilized sand dunes. In addition, ant burrows are very common in modern eolian environments (Whitford, 2002); however, their fossil record is scarce. The absence of ant burrows is most likely related to the low preservation potential of these structures (Genise and Bown, 1994). Other arthropods produce trails that are not connected with the surface (closed), moving below the surface for refuge from the heat and potential enemies through the process of sand swimming (Whitford, 2002). Some well-known recent producers of closed excavations are beetles (Scarabaeidae, Tenebrionidae, and Histeridae) and desert cockroaches (Polyphagidae) (Phelps, 2002). The sand swimming mechanism usually produces unlined and massively infilled close burrows (Phelps, 2002). The sand swimming organisms are most likely limited to moderately dry sediment, since wet sands would offer more resistance. Conversely, open excavation systems may be produced in wet or dry sands, and may possess or lack a wall lining. For example, some spiders use their webs to stabilize the burrows, which may be preserved as lined burrows, whereas the meniscate infill seems to be most likely produced in areas with higher moisture content (Phelps, 2002).

Even though Cenozoic tetrapod footprints in deposits related to deserts are not deeply understood, the number of case studies is enough to make some generalizations. Footprints of large-sized mammals, such as artiodactyls, perissodactyls, and proboscideans, are common in dune and interdune deposits since the late Eocene–early Miocene. Other common elements are footprints of medium-size mammals, rodents, turtles, and carnivorans (Fornós et al., 2002; Lea, 1996; Phelps, 2002; Roberts et al., 2008; Smith and Mason, 1998). Deposits from inland deserts and coastal deserts in South America mostly contain fossil footprints from Miocene and Pliocene times. Footprints of large and medium-sized megatheriid ground sloths, macraucheniid and proteroteriid litopterns, marsupial sabre-toothed tiger, capybara rodents, phorusrhacids and flamingos, and medium to small-sized rodents and shorebirds (Fig. 14) (Ahumada, 2004; Angulo and Casamiquela, 1982; Aramayo, 2007; Casamiquela, 1974; Krapovickas and Vizcaíno, in press; Leonardi, 1994; Melchor et al., 2015; Zavattieri et al., 2001).

Large burrows produced by tetrapods, mostly mammals and reptiles, but also amphibians, are still common during the Cenozoic, and are well documented in modern examples. Open burrow systems with meniscate backfill are produced by armadillos in Miocene and Holocene

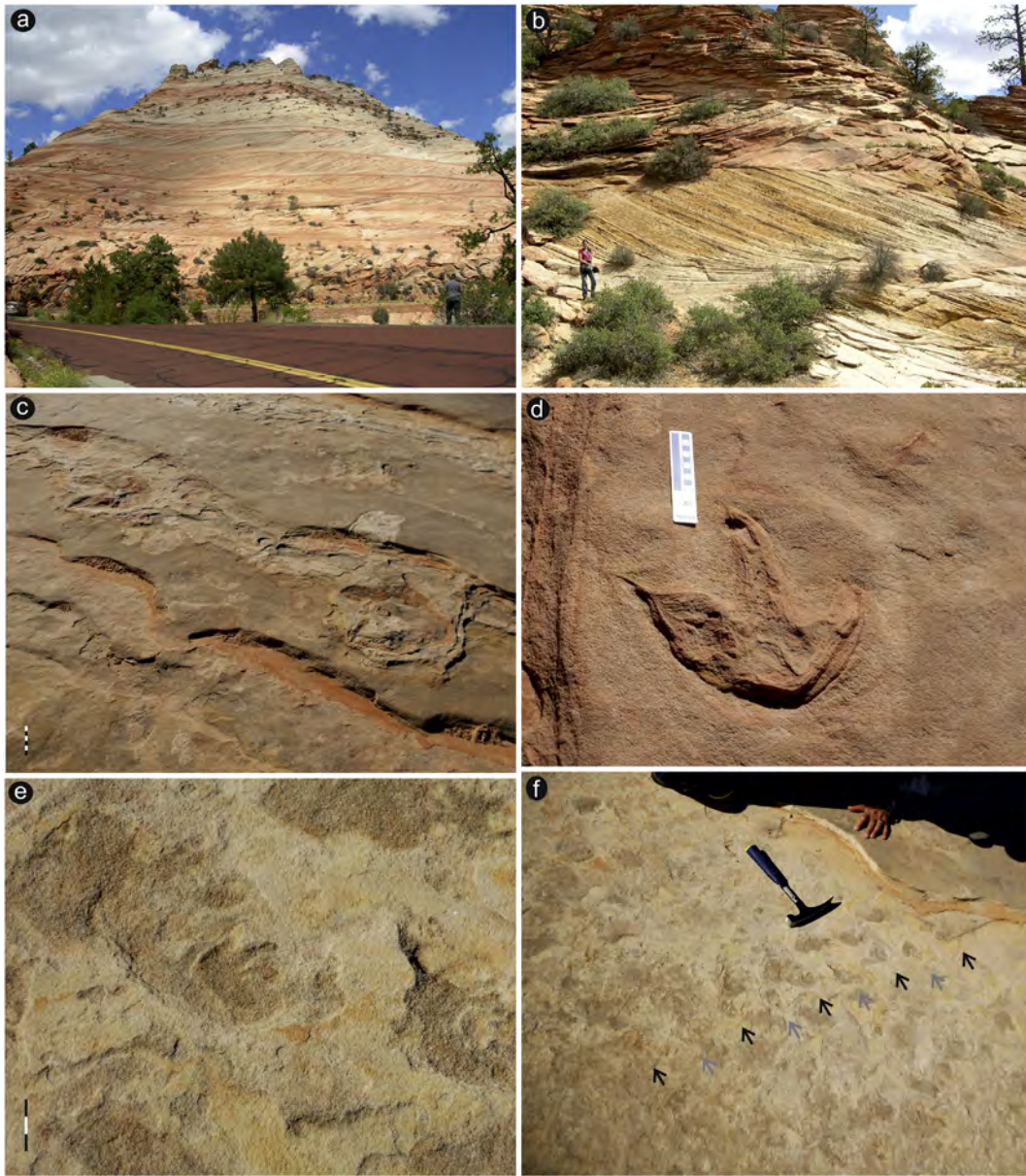


Fig. 8. Lower Jurassic Navajo Sandstone of the Zion National Park Utah. a, b: General view of large-scale cross-bedded sandstone units recording deposition due to migration of eolian dunes. c–f: Trackways preserved at Moccasin Mountain tracksite, Utah. c: General view of a trackway of *Eubrontes*. d: Detail of view *Eubrontes*. e: Detail of view of *Batrachopus*. f: General view of a trackway of *Batrachopus*.

wet and dry interdune deposits of Argentina (Melchor et al., 2012b). Hembree and Hasiotis, 2007 demonstrated that sand swimming snakes produce a wide variety of biogenic structures in unconsolidated sand typical of arid and semiarid climates, but these structures have not been recognized in the fossil record so far.

A number of papers have documented the ichnology of modern and Quaternary coastal-dune calcarenites in tropical settings, particularly in San Salvador Island, Bahamas (Curran and White, 2001, 1991; Curran, 2007, 1994, 1992, 1984; Curran et al., 2016), where the *Celliforma* Ichnofacies has been identified. Root traces are extremely abundant in deposits of vegetated dunes, in places leading to intense disruption of the sedimentary fabric (Fig. 15a–b). Other trace fossils are produced by a variety of arthropods, including vertical burrows (*Skolithos*) attributed to insects or spiders (Fig. 15d–e), trackways (*Coenobichnus*) of land hermit crabs (Walker et al., 2003), and burrows constructed by the land crab *Gecarcinus lateralis* (Seike and Curran, 2010). In addition, various enigmatic structures of more debatable affinities have been identified, including cluster burrows (Fig. 15f) attributed to sphecid wasps

and stellate burrows similar to those produced by halictid bees (Fig. 15g–h) (Curran, 2007; Curran et al., 2016). Marine crab burrows are represented by the ichnogenus *Psilonichnus*, which typically occur in backshore beach deposits rather than in the coastal dunes themselves, representing the *Psilonichnus* Ichnofacies (Curran, 2007) (Fig. 15c). Similar eolian calcarenites to those documented from Bahamas are known elsewhere, including Quaternary coastal dune deposits containing abundant root trace fossils (Fig. 16a–b) in the Mayan Riviera of Mexico (Kelley et al., 2006) and root trace fossils and crab burrows (Fig. 17a–d) in Kaua'i, Hawai'i (Blay and Longman, 2001).

4. Desert megatrends

Ecosystems result from the interaction between their physical, chemical, and biological worlds (e.g. Ricklefs and Miller, 2000). Beyond the patterns observed today, ecosystems have deep historical roots and many aspects have changed through time, such as the taxonomic composition and diversity of their communities and environments.

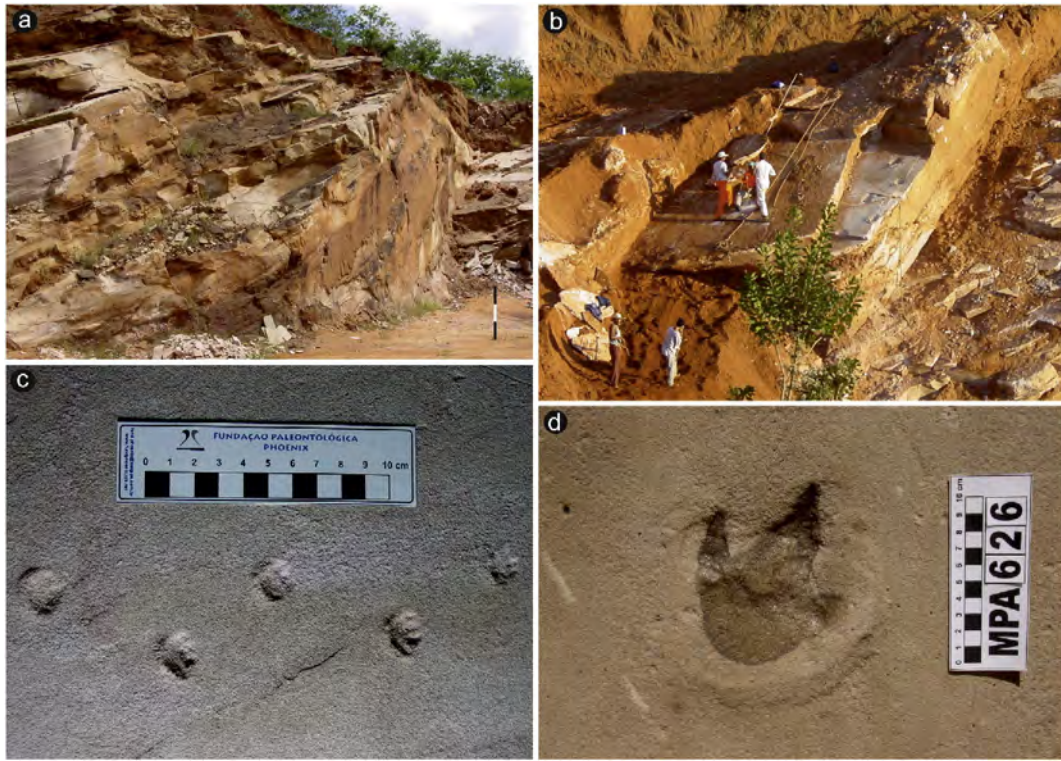


Fig. 9. Lower Cretaceous Botucatu Formation of Brazil. a, b: General view of trace fossil-bearing locality at São Bento quarry, located in the city of Araraquara, São Paulo state. b: General view of an ornithomimid trackway. c: *Brasilichnium elusivum*. d: Theropod footprint. The scale bar is 160 cm. Photographs courtesy of Marcelo A. Fernandes.

Therefore, the assemblages of organisms are constantly accommodating and changing in character as the result of the evolution of species and extinction, but also due to environmental change, and immigration and emigration of taxa, among others (see [Bambach and Bennington, 1996](#)). Paleocologists can document these long-term paleocommunity variations through the analysis of the body and trace fossil records. Desert biotas have a strong ichnologic signal and thus, are suitable to be analyzed through geological time. Our systematic review of the ichnologic record of desert environments allows the proposal of a model involving five main phases of colonization.

4.1. Phase 1. Incursions into coastal deserts

The first phase in the colonization of deserts is coincident with the initial phase of terrestrialization that occurred during the early Paleozoic (Cambrian–Silurian). It involved animal incursion into coastal dune fields directly from the sea, although it is unlikely that these animals would have remained for long periods of time in coastal deserts ([Fig. 18](#)). This is recorded by superficial trackways produced by amphibious arthropods (e.g. [Hagadorn et al., 2011](#); [MacNaughton et al., 2002](#); [Trewin and McNamara, 1994](#); [McNamara, 2014](#)). The first tentative excursions out of the sea were made by euthycarcinoids by the middle Cambrian ([Collette et al., 2012](#); [Hagadorn et al., 2011](#)). Younger examples on coastal deserts were also interpreted as produced by euthycarcinoids (e.g. [MacNaughton et al., 2002](#); [Trewin and McNamara, 1994](#)). This is not the only arthropod group that undertook excursions out of the sea, and other taxa, such as eurypterids, scorpions, and myriapods, have also been proposed to have walked or burrowed in terrestrial settings ([Braddy, 2004](#); [Trewin and McNamara, 1994](#); [McNamara, 2014](#)).

There are several proposed hypotheses about why arthropods invaded the land and different groups could have had different triggers ([Braddy, 2004](#)). Some of these hypotheses include avoiding predation

([Trewin and McNamara, 1994](#)), occupation of a new empty ecospace ([Buatois et al., 1998](#)), incursion in harsh environments in order to mate and/or spawn ([Braddy, 2001](#)), and/or simply to move from one intertidal pool to another ([Hagadorn et al., 2011](#)).

4.2. Phase 2. Arthropod incursions/colonization of inland deserts

Even though the first steps into land occurred as early as the middle Cambrian, ichnologic evidence suggests that major colonization of coastal settings and other terrestrial settings did not take place until the Early Devonian, showing consistency with the body fossil record ([Braddy, 2004](#); [Minter et al., 2016b](#)) ([Fig. 18](#)). The ichnologic record most likely reflects the activities of dune pioneers that left their fluvial habitat to enter temporary or permanently into inland deserts. Stem-group arachnids (i.e. stylonurid eurypterids) or arachnids (scorpions) are interpreted as actual inland desert inhabitants together with myriapodous arthropods, probably eoarthropods ([Morrissey et al., 2012](#)). Superficial trackways produced by these organisms are the dominant element in Devonian deserts. Although scarce, sub-superficial arthropod behavior was already present by that time. It mostly corresponds to sub-horizontal activity just under the surface of the sand and short vertical excavations ([Morrissey et al., 2012](#)).

So far, there is no evidence of plant colonization of deserts by Devonian times so this would rule out the presence of herbivorous in these environments, even though they were already present elsewhere by that time ([Labandeira, 2005](#)). Accordingly, the question about what desert inhabitants were feeding on arises. It could be said that detritivory and carnivory were present in desert food webs. It has been proposed that winds provided deserts with small detritus particles thus resulting in new food resources available for the emergent desert inhabitants ([Morrissey et al., 2012](#)). Apart from this, carnivorous animals were also present, probably represented by stem-arachnids and/or scorpions.

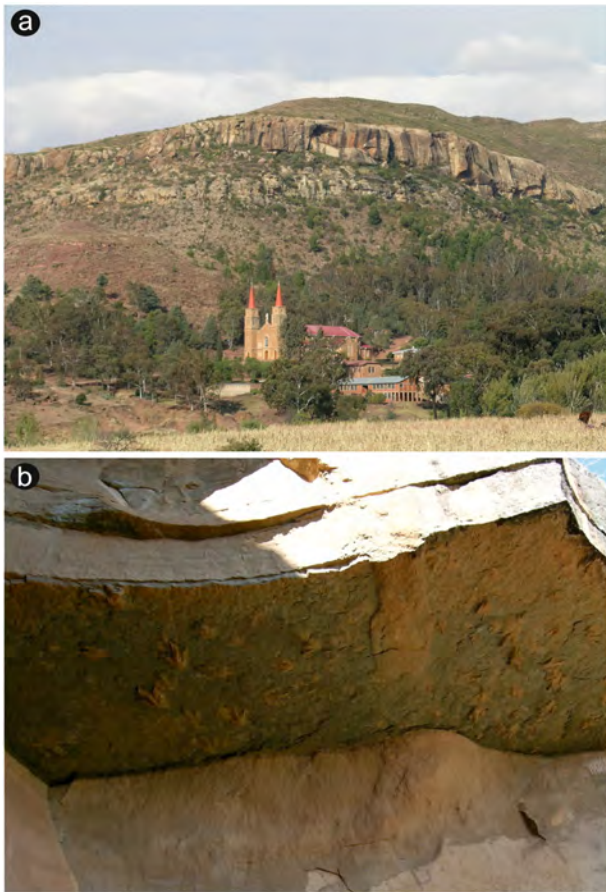


Fig. 10. Lower Jurassic Clarens Formation of Southern Africa. a. General view of the outcrops. b: Detail view of theropod footprints preserved as positive hyporelief. Photographs courtesy of Roger Smith.

4.3. Phase 3. Tetrapod colonization of deserts

The third phase in the colonization of deserts started during the Carboniferous but peaked at the earliest Permian and involved the colonization of deserts by tetrapods (e.g. Gilmore, 1928, 1927, 1926; Krapovickas, 2010; Krapovickas et al., 2015; Lockley and Hunt, 1995; Mckeever and Haubold, 1996; Mckeever, 1991). The invasion of deserts by tetrapods encompasses the culmination of a protracted process that began when tetrapods left subaqueous lacustrine and marginal-marine settings by the Middle–Late Devonian (e.g. Clack, 1997; Niedźwiedzki et al., 2010; Stössel, 1995). The dominant groups within the first colonizers in deserts are the synapsids, the mammalian evolutionary line. Interestingly, the Permian tracks attributed to non-mammalian synapsids reflect highly comparable patterns of locomotion while moving through eolian dunes with those described from Mesozoic deserts attributed to mammaliaforms (Fig. 18).

In late Paleozoic deserts, the patterns of invertebrate bioturbation still resemble those of the middle Paleozoic, in that there was limited colonization of the infaunal ecospace in eolian dunes, even though evidence of animal activity is more widespread. Superficial arthropod locomotion structures are dominant elements within late Paleozoic deserts, particularly those produced by spiders and scorpions (Brady, 1961, 1947). The record of insect behavior is barren in late Paleozoic desert deposits. Subsuperficial activity is also present but still playing a minor role

The first steps in the colonization of deserts by plants date back to the Middle Pennsylvanian when plants colonized stabilized deflation surfaces within coastal deserts (Loope, 1988, 1985). Nevertheless, they

were apparently incapable of colonizing and stabilizing mobile eolian dunes (Loope, 1988).

4.4. Phase 4. Major infaunal colonization

During the Mesozoic inland deserts experienced a significant turnover that involved a major exploitation of the infaunal ecospace as reflected by the appearance of more varied behavioral patterns in sub-superficial structures (Fig. 18). Sub-superficial activity in deserts is highly beneficial because sand is a poor conductor of heat. Animals inhabiting areas beneath the surface, even at shallow depths, experience temperatures suitable for survival in both hot and cold days (Crawford, 1988). Nevertheless, organisms that inhabit modern deserts produce burrows for a large variety of purposes, including dwelling, nourishment, larval development, reproduction, thermal protection, osmotic regulation, and/or protection against predators, among others (Crawford, 1981). Sub-superficial activity of holometabolous insects, such as beetles and hymenopterans, as well as arachnids, is dominant and superficial arthropod trackways are almost absent in Mesozoic eolian deposits (Ekdale and Picard, 1985; Ekdale et al., 2007). Early Mesozoic desert ecosystems were enriched with modern arthropod lineages as hemipteroid and holometabolous insects. This is congruent with the establishment of the modern insect fauna by the earliest Mesozoic with insects as the dominant terrestrial group in lowland ecosystems (Labandeira and Sepkoski, 1993). Major diversification within insect lineages, such as ants and beetles, occurred by the end of the Mesozoic, mostly coupled with angiosperm appearance (e.g. Farrell, 1998; Moreau et al., 2006), which likely impacted on the increase of intensity of bioturbation.

Previous ideas about the colonization of deserts by plants proposed that sediment-penetrating plants were adapted to live in mobile sand dunes of arid deserts since the Cenozoic (Glennie and Evamy, 1968). However, this view has been challenged by data published in the last thirty years that evidence the presence of rooted plants in Middle Jurassic mobile eolian dunes (Loope, 2008, 2006a).

Aridity and seasonality played a fundamental role in selecting tetrapod burrowing behavior (Krapovickas et al., 2013). Burrows are particularly abundant in Permian and Triassic arid overbank settings, possibly implying that burrowing strategies on more stable substrates were attained earlier than on shifting sands (e.g. Colombi et al., 2008; Dentzien-Dias, 2010; Krapovickas et al., 2013; Miller et al., 2001; Smith and Botha, 2005; Smith and Swart, 2002; Smith, 1987; Voigt et al., 2011). Since the Jurassic, tetrapod burrows became a significant element within deserts, even though they were already present in Permian deserts (e.g. Bordy and Catuneanu, 2002; Clemmensen and Abrahamsen, 1983; Dentzien-Dias et al., 2007).

4.5. Phase 5. Establishment of modern desert communities

Since the late Mesozoic and mostly through the early Cenozoic, the ecological dynamic of modern desert communities was already attained. The ecospace was fully occupied even though the modern magnitude of activity and indeed the higher bioturbation indexes were achieved not until the Neogene. The behavior of ancient animals recorded in these sediments is diverse, and numerous dwelling, locomotion, feeding, hatching, and nesting strategies are recorded (Fig. 18).

Ants are the most abundant surface-active arthropods of modern deserts, but it is not until the Neogene that ants attained a main role within desert communities (e.g. Smith et al., 2011). Ants, as well as termites, are most of the time in underground galleries (Whitford, 2002). Beetles are the group of surface-active arthropods that follow in abundance, being darklings especially common (Whitford, 2002). Particularly, they inhabit sand dune areas and are detritus feeders, like other sand diggers organisms, such as some members of Orthoptera (Crawford, 1988). The arachnids (spiders, scorpions and solifuges) are important



Fig. 11. Lower Cretaceous Djadokhta Formation of Mongolia. a–b: *Entradichnus meniscus* oriented parallel to the depositional dip on foresets of large-scale cross-stratified strata. c–d: Detail view of *E. meniscus*. Photographs courtesy of Koji Seike.

predators, and are the third main group of surface-active arthropods in recent deserts. Many of their excavations occur as part of their feeding strategy, waiting for the right time for prey capture by adopting the strategy of “sit and wait” (Whitford, 2002). For instance, subterranean

termites are the dominant macrofauna of arid soils (Crawford et al., 1993). Earthworms are prevalent elements of some desert soils, especially in those with high silt content (Crawford et al., 1993). Among vertebrate predators, lizards are the most abundant in today's

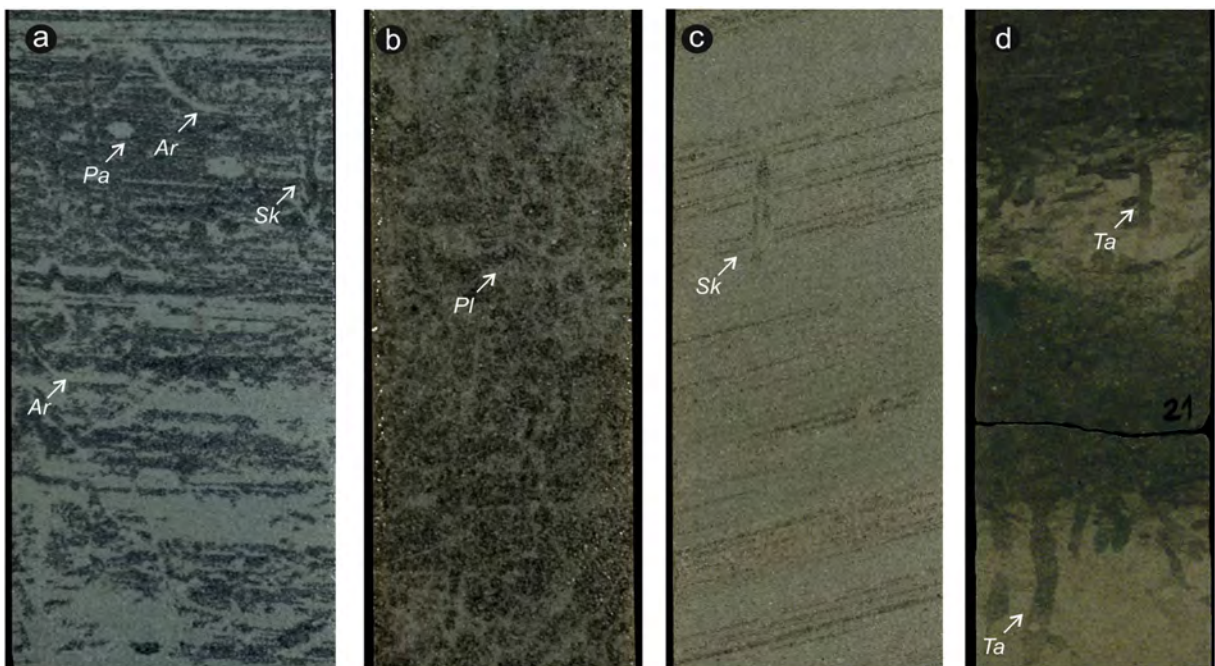


Fig. 12. Core photographs from the Lower Cretaceous Mulichinco Formation of Argentina. a. Eolian dune deposits containing *Arenicolites* (*Ar*), *Skolithos* (*Sk*), and *Palaeophycus* (*Pa*). b. Eolian sand sheet deposits with a mottled texture attributed to *Planolites* (*Pl*). c. Eolian sand sheet deposits with *Skolithos* (*Sk*). d. Sheet-like sandstones of fluvial origin displaying *Taenidium* (*Ta*). Core width is 7.5 cm.

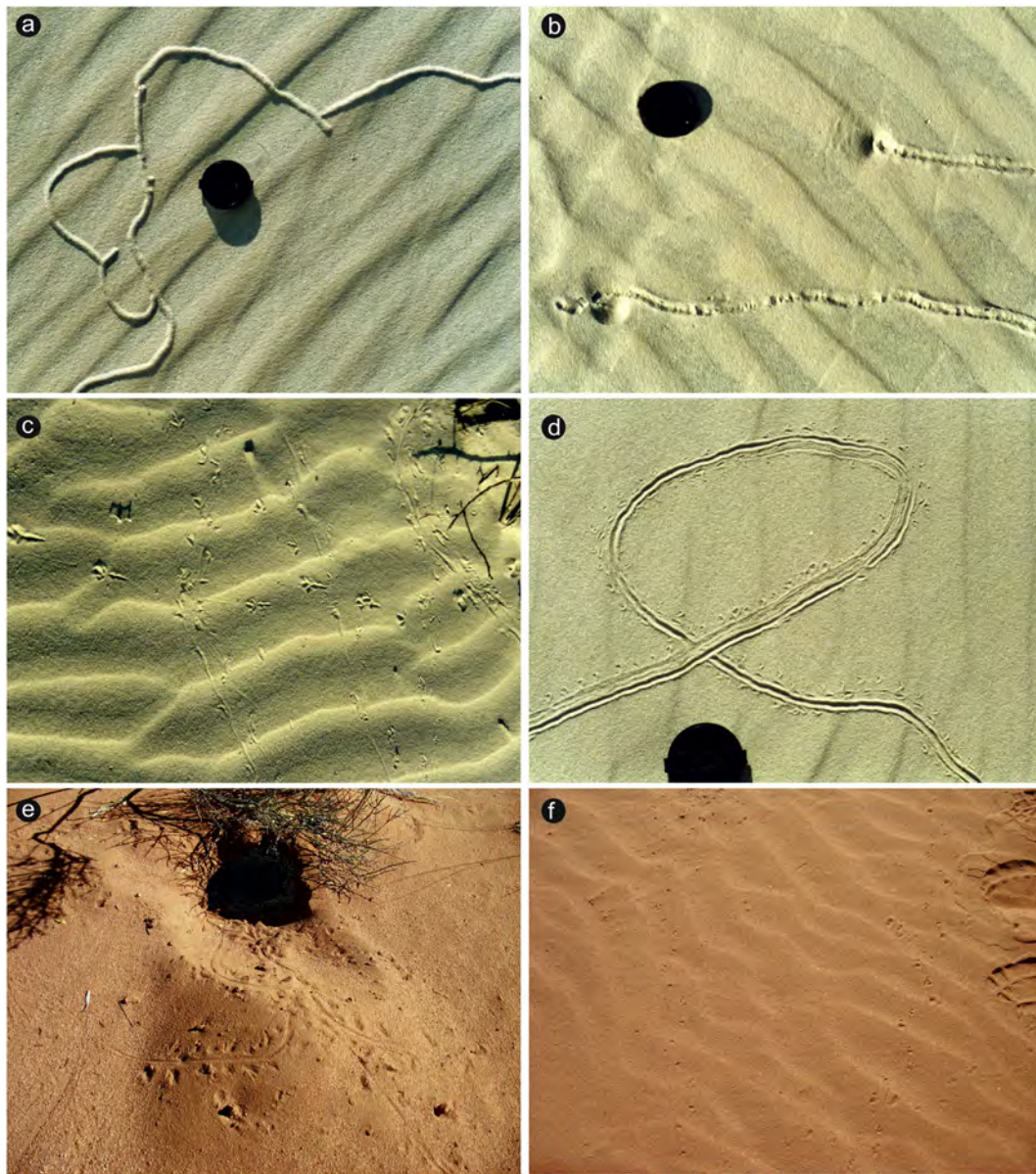


Fig. 13. Modern invertebrate and vertebrate traces on eolian environments. a–d: Traces on recent backshore dry interdunes of Brazil. a–b: Beetle burrows. c: Bird trackway. d: Beetle trackway. e–f: Inland dunes of Argentina. e: Abandoned tetrapod burrow occupied by a lizard and denoted by its trackways. f: Recent arachnid trackway comparable with *Octopodichmus*. Photographs a–d courtesy of Renata Netto.

deserts, with two classes of feeding strategies: “sit and wait”, and widely foraging predators (Huey and Pianka, 1981).

In recent deserts, burrowing is a common strategy among tetrapods and a large number of mammals, reptiles, amphibians, and even birds dig burrows or use those produced by other animals (Kinlaw, 1999). Moreover, burrows are an important feature of deserts by producing patchiness that facilitates plant growing and pedogenesis (Ahlbrandt et al., 1978). Most small-sized mammals produce excavations where they spend most of the day (Whitford, 2002). Burrows could be simple to complex, such as those produced by the kangaroo rat (Whitford and Kay, 1999). Mammals of medium size, such as foxes or hares, can generate their own excavations, enlarge or re-use those of others, or take shelter under the shade of shrubs or small trees (Whitford, 2002). Reptiles frequently maintain constant body temperature changing between sunlight and shaded areas. In dune environments without shadows or shelters provided by vegetation, certain snakes and lizards “swim” in the sand to avoid overheating (Hembree and Hasiotis, 2007). Even though amphibians are unlikely inhabitants of deserts due to their

strong limitations to retain water, they are present in the world’s hot deserts where they excavate to avoid desiccation (Ahlbrandt et al., 1978; Whitford, 2002).

5. Vertebrate and invertebrate eolian ichnofacies revisited

In spite of the changes evidenced by desertic biotas and their associated biogenic structures during the Phanerozoic, it is possible to find common characteristics among invertebrate and vertebrate ichnofaunas through time, thus allowing the refinement of the known eolian ichnofacies models (Fig. 19).

The invertebrate ichnofacies for eolian dunes is re-named herein as the “*Octopodichmus–Entradichnus* Ichnofacies” honoring the seminal work of Hunt and Lucas (2007a) and Ekdale et al. (2007), who simultaneously tackled the issue of eolian dune ichnofacies, albeit arriving at somewhat different conclusions (see also Buatois and Mángano, 2011). This ichnofacies is characterized by (1) low-to more rarely moderate ichnodiversity, particularly in post-Paleozoic

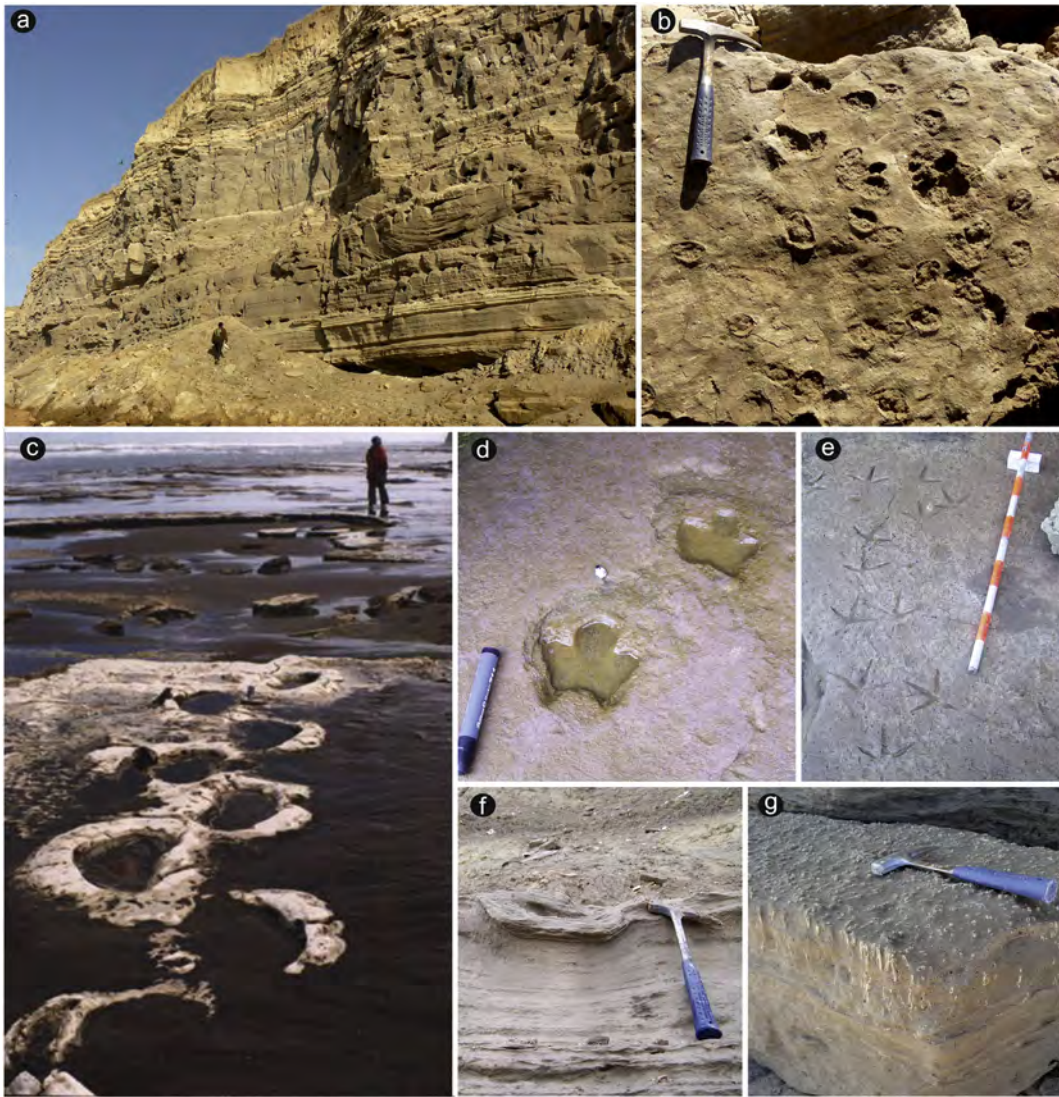


Fig. 14. Upper Miocene Rio Negro Formation of Argentina. a: General view of an eolian dune–interdune system with large-scale cross-bedded sandstones recording deposition due to dune migration and parallel lamination related to interdune accumulation. b: Unionid bivalves resting structures. c: *Megatherichnum oportoii*, trackway produced by megatheriid ground sloths. d: *Macrauchenichnus* isp., footprints produced by macraucheniid litopterns e: Bird footprints. f: Footprint in cross section. g: Abundant vertical tubes on interdune facies. Photographs courtesy of José Cuitiño, Noelia Carmona, and Silvia Aramayo.

examples; (2) dominance of simple sub-superficial dwelling traces produced mostly by members of Coleoptera, Orthoptera and Arachnida, with horizontal (e.g., *Palaeophycus*) and/or vertical orientation (e.g., *Skolithos*, *Digitichnus*); (3) superficial locomotion traces produced by arthropods, especially arachnids (e.g., *Octopodichnus*, *Paleohelcura*); and (4) subordinate feeding simple (*Planolites*) and meniscate (e.g., *Taenidium*, *Entradichnus*) traces.

The *Octopodichnus*–*Entradichnus* Ichnofacies occurs in mobile and temporary stabilized sandy substrates, subject to frequent erosion and deposition, and to strong seasonality. This ichnofacies is characteristic of environments with reduced humidity (rate of evapotranspiration exceeds precipitation for most of the year), and a low nutrient availability. The ichnofacies mostly occurs in sand dune, dry interdune, and sand sheet deposits of wet eolian systems typical of arid deserts and/or in arid intervals of hyper-arid deserts.

The vertebrate ichnofacies of deserts maintains the original denomination of Hunt and Lucas (2007a): the *Chelichnus* Ichnofacies. The ichnofacies ranges from the early Permian to the Holocene and reflects profound changes in taxonomic composition due to faunal turnovers within deserts. During the late Paleozoic, the *Chelichnus* Ichnofacies is mostly exclusively composed of footprints of non-

mammalian synapsids (*Chelichnus*) and locally tetrapod burrows and scarce reptile footprints. This ichnofacies displays a marked change in its composition toward the Mesozoic which is dominated by footprints of medium sized non-avian theropod dinosaurs (*Grallator*) (Lockley et al., 2007), mammaliaform footprints (*Brasilichnium*) and burrows (mostly in semi-arid) and subordinated medium and large-sized non-avian theropod dinosaurs (*Anchisauripus*, *Eubrontes*). During the Cenozoic, particularly in the Neogene, desert ichnofaunas had a similar structure to that of modern environments, including dominance of footprints of medium-sized mammals and rodent excavations with subordinate tracks of large-sized, both herbivorous and carnivorous, mammals.

The *Chelichnus* Ichnofacies occurs in sandy deserts with reduced humidity (rate of evapotranspiration exceeds precipitation for most of the year), and low nutrient availability, as arid deserts and/or in arid intervals of hyper-arid deserts. Interaction of precipitation and nutrient availability is critical in controlling the presence of the *Chelichnus* Ichnofacies in desertic environments. This ichnofacies is recorded in sand dune, dry interdune, and sand sheet deposits of wet eolian systems, but also in laterally adjacent alluvial and lacustrine depositional settings.

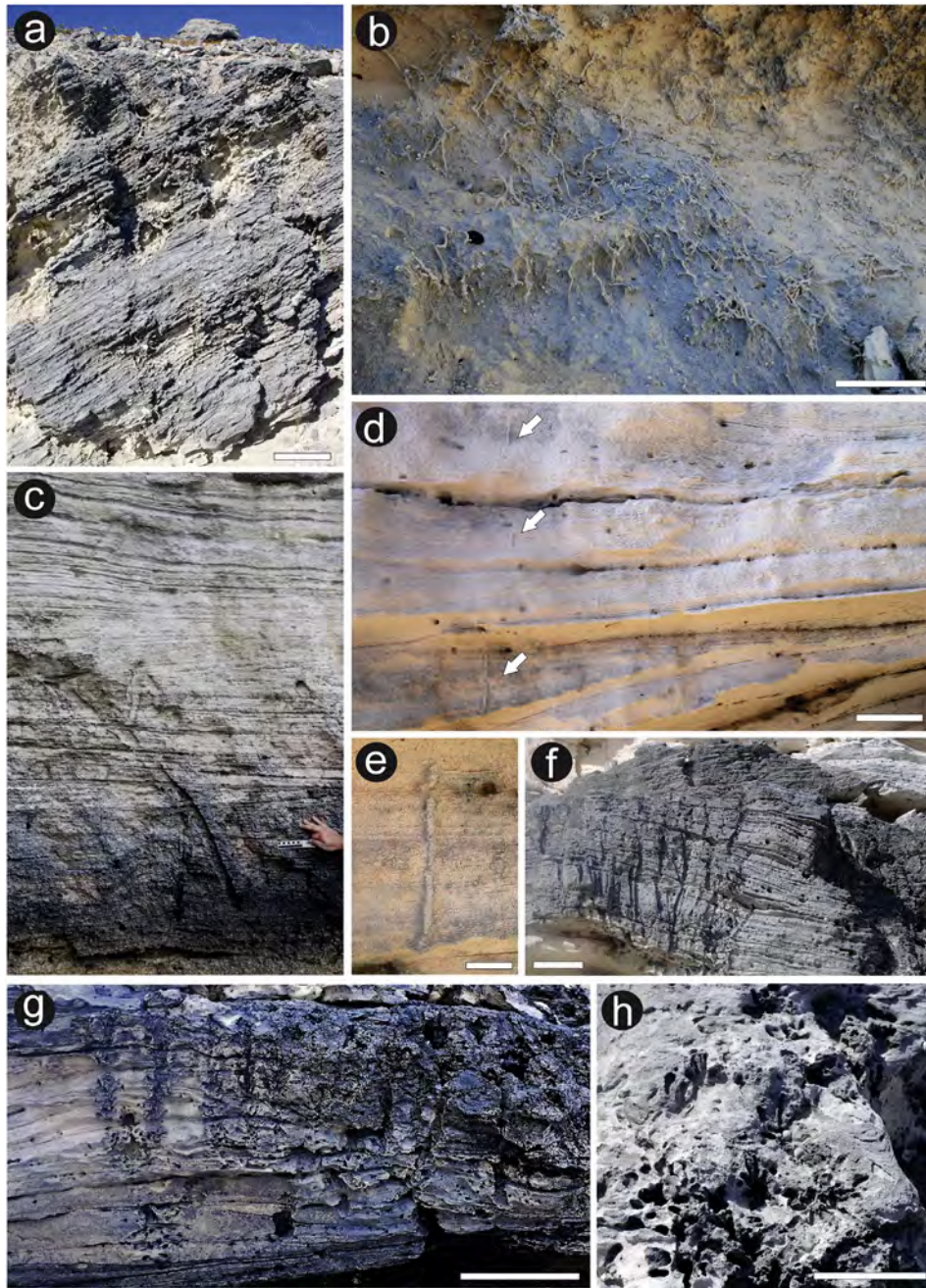


Fig. 15. Trace fossils of Quaternary coastal-dune calcarenites, San Salvador Island, Bahamas. a: High angle cross-stratified calcarenites with rhizoliths penetrating from the top of the deposit. Pleistocene, Cockburn Town Member, Grotto Beach Formation, The Gulf. Scale bar is 50 cm. b: Close-up view showing high density of rhizoliths. Pleistocene, Cockburn Town Member, Grotto Beach Formation, The Gulf. Scale bar is 20 cm. c: *Psilonichnus upsilon* in cross-stratified calcarenites. Holocene, Hanna Bay Member, Rice Bay Formation, Hanna Bay. d: Cross-stratified calcarenites with vertical insect or arachnid burrows attributed to *Skolithos* (arrows). Holocene, Hanna Bay Member, Rice Bay Formation, Hanna Bay. Scale bar is 10 cm. e: Close-up view of a *Skolithos* specimen, Hanna Bay. Scale bar is 1 cm. f: Cluster burrows probably produced by sphecid wasps. Holocene, Hanna Bay Member, Rice Bay Formation, Hanna Bay. Scale bar is 20 cm. g: Cross-section view of stellate burrows attributed to halictid bees. Holocene, Hanna Bay Member, Rice Bay Formation, Hanna Bay. Scale bar is 40 cm. h: Bedding-plane view of the stellate burrows. Holocene, Hanna Bay Member, Rice Bay Formation, Hanna Bay. Scale bar is 20 cm.

The case of the *Chelichnus* and *Entradichnus*–*Octopodichnus* Ichnofacies occurring under the same environmental parameters is an exception among vertebrate and invertebrate ichnofacies. The distribution of tetrapod footprints and invertebrate trace fossils does not seem to be controlled by the same paleoenvironmental factors (Krapovickas, 2010). Animal behavior on a landscape is essentially determined by organism size and the scale at which animals interact with the landscape. A landscape feature, such as a river margin, can be a corridor for some species, a barrier for others species, and a neutral feature for others (Allen and Hoekstra, 1990). As such, although local environmental parameters are involved in the distribution of

invertebrate trace fossils, the distribution of tetrapod trace fossils in terrestrial environments seems to be more related to key environmental regional-scale parameters, such as climate and resource availability (Krapovickas et al., 2010).

6. Desert landscape units and trace fossil distribution

Ecosystems are composed of landscape units in which biotic and abiotic processes interact. Desert settings consist of complex mosaics of habitats or physical units associated with the activity of the organisms that inhabit them, changing the availability of key resources, such as



Fig. 16. Coastal-dune calcarenites, Pleistocene of Tulum, Mayan Riviera, Mexico. a: High angle cross-stratified calcarenites with rhizoliths penetrating from the top of the deposit showing the establishment of a paleosol. b: Close-up view of the top of the deposit showing relatively high density of rhizoliths. Scale bar is 15 cm.

water and nutrients (see Whitford, 2002). In this section, we analyze the distribution of trace fossils in deserts as a mosaic of units with different physical and biotic characteristics. The landscape units here defined are based on water content and its temporal fluctuations, nutrient availability, nature of the substrate, and the dominant organisms present.

6.1. Eolian dunes, interdunes, and sand sheets

Dunes, interdunes, and sand sheets share several physical and biological elements, conforming a single landscape unit. They consist of sandy substrates of variable mobility, reduced humidity, and low nutrient availability. Eolian deposits and bedforms occur in deserts where there is abundance of sand and dust, sufficient wind energy to transport the material, and conditions favoring their accumulation (Lancaster, 1995). Dunes migrate downwind as a consequence of sand being swept from the stoss slope, taken by the airflow, and deposited on the lee slope. As the airflow moves over the dune, it separates onto the lee slope and decelerates, resulting in grain fall-out from suspension; episodically the surfaces become unstable and collapse, causing dune migration over time (Mountney, 2006). Because of their mobile nature, dunes have been largely misunderstood as almost devoid of life. However, recent and fossil records indicate that dunes have diverse inhabitants with numerous ethologic strategies. Interdunes are flattened areas of variable dimensions within eolian dune fields (Lancaster, 1995). Eolian ripple strata are widespread on dry surfaces and commonly contain abundant plant and animal bioturbation structures. Extensive

areas of low relief lacking eolian dunes are known as sand sheets, dominated by wind-rippled sand and develop in areas where transportable sand is deficient due to grain-size or high water table (Mountney, 2004).

This is the landscape unit most widely represented in hyper-arid and arid deserts. As mentioned above, under arid conditions, this unit mostly hosts sub-superficial dwelling trace fossils and surficial locomotion traces ascribed to the *Octopodichnus*–*Entradichnus* Ichnofacies and tetrapod footprints and burrows ascribed to the *Chelichnus* Ichnofacies (Figs. 20, 21).

When the moisture content in these environments is sufficient to support a plant community, root traces may occur (Loope, 2008, 2006a; Loope et al., 1998; Tanner et al., 2006). Commonly, arthropod excavations are concentrated in areas of major vegetation development, which not only provide a more appropriate microclimate and stabilized sediments, but also plant parts and organic material for feeding or hunting organisms frequent in those areas (see Whitford, 2002).

6.2. Wet interdunes

Ephemeral water bodies of different configurations and sizes are commonly present in deserts (Crawford, 1981). In interdune low areas after heavy rainfall events, ephemeral ponds, which are sporadic aquatic systems, are commonly established (Whitford, 2002). This landscape unit presents a variety of sedimentary structures typical of subaqueous deposition or post-depositional soft-sediment deformation (Mountney, 2006, 2004). The high water table produces local concentration of plant roots, tetrapod footprints, and invertebrate traces in wet interdunes (Buatois and Mángano, 2011). The tetrapod footprint record is virtually indistinguishable from that of dune, dry interdune, and sand-sheet environments and certainly constitutes part of the *Chelichnus* Ichnofacies (Fig. 21). Footprints produced in wet interdunes occur in soft sediment and the preservation could vary depending on the degree of water saturation present when the footprint was formed (Seiler and Chan, 2008). On the contrary, invertebrate trace fossils mostly correspond to assemblages of semiaquatic organisms that produce vertical dwelling, locomotion, grazing, and feeding structures and may correspond to the *Scoyenia* Ichnofacies (Figs. 21, 22) (Buatois and Mángano, 2004). In subaqueous continental settings, vertical small straight and U-shaped burrows are commonly interpreted as produced by dipterous larvae (mostly midges), as well as small oligochaeta (e.g. Chamberlain, 1975; Netto, 2007; Rindsberg and Kopaska-Merkel, 2005; Schirf et al., 2001; Uchman, 2005). Chironomids comprise one of the most abundant and diverse aquatic group of Diptera in modern continental environment (Paggi, 2001). Their larval stages are subaqueous and live in tubes within the sediment, usually in places protected from strong currents (Paggi, 2001). Some annelids are important components of existing benthic faunas (e.g. Tubificidae), and produce delicate shallow excavations both on sandy and muddy substrates where they feed on detritus, bacteria, and algae (Cohen, 2003). Crane fly larvae produce surficial grazing traces and small meniscate traces in continental arid environments (Ahlbrandt et al., 1978). Similarly, certain freshwater gastropods inhabitant of small interdune ponds produce surficial grazing traces similar to *Gordia* or *Archaeonassa* (Ahlbrandt et al., 1978). Surficial to sub-superficial locomotion traces, such as *Cruziana*, are common in shallow sporadically flooded water bodies and have been interpreted as produced more likely by notostracans (Bromley and Asgaard, 1972; Pollard, 1985). Notostracans are typical components of today's ephemeral water systems; they quickly colonize these new habitats, exploiting the high concentration of organic matter available after the flooding event has passed (e.g. Whitford, 2002).

6.3. Playa lake

Playa lakes form in depressed topographic areas that during the wet season or after episodic flooding events are charged with water through

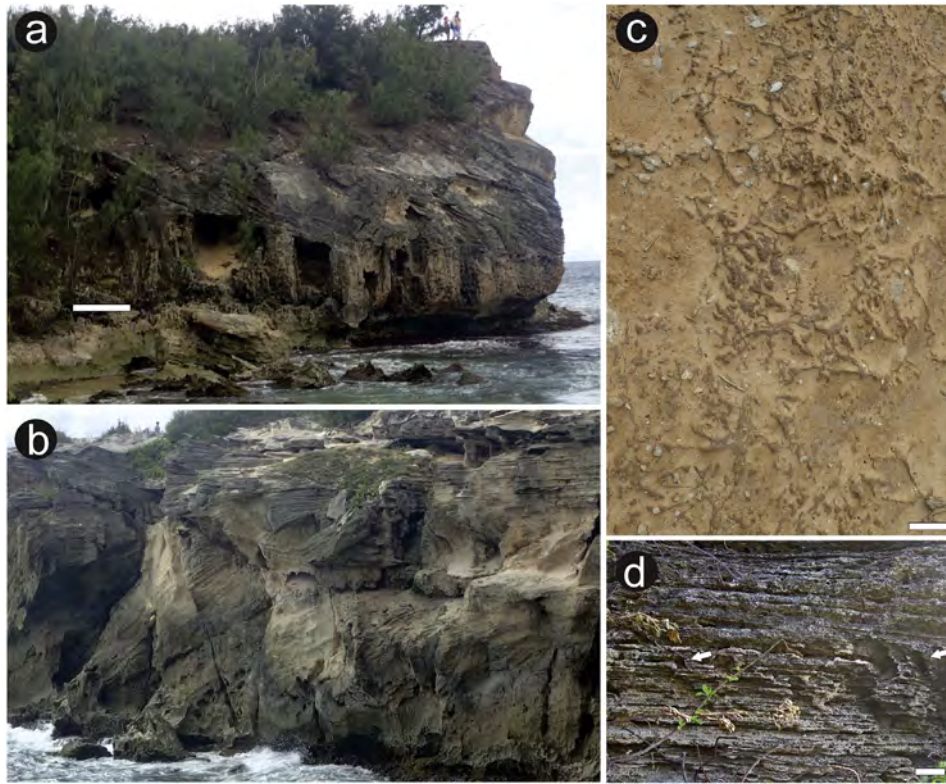


Fig. 17. Coastal-dune calcarenites, Late Pleistocene–Holocene Māhā‘ulepū Formation in Makawehi Point, Kaua‘i, Hawai‘i. a: General view of high angle cross-stratified calcarenites. b: Close-up view of cross-bedded eolian sets. c: Bedding-plane view of rhizoliths. Scale bar is 20 cm. d: Cross-stratified calcarenite showing poorly preserved, open crab burrows (arrowed). Scale bar is 15 cm.

either surface stream flow or groundwater recharge (Mountney, 2004). During dry periods (regressive), they are subject to strong evaporation and lake level reduction, producing brine pools and subsequent salt precipitation. By contrast, during the wet periods (transgressive) there is more freshwater available without evaporite precipitation (Alonso, 2006). During drought periods, groundwater level can be well below the surface, so playa lakes dry up and are invaded by eolian sands involving lacustrine and eolian processes as well as chemical precipitation (Alonso, 2006); depending on these conditions playa lakes may be vegetated or not (Whitford, 2002). These unstable environments have low bioturbation intensities and trace fossils may develop at the pool margins (Buatois and Mángano, 2009). During regressive phases, playa-lake deposits contain almost exclusively surficial arthropod locomotion trace fossils, such as *Paleohelcura* (Fig. 21) (e.g. Kozur et al.,

1994). On the other hand, during the transgressive phases, with freshwater dominance, invertebrate traces correspond to simple dwelling (*Palaeophycus*) and meniscate feeding traces (*Taenidium*), ascribed to the *Scoyenia* Ichnofacies (Fig. 22). Paleozoic examples of tetrapod footprints are scarce, and mostly correspond to non-mammalian synapsids of the *Chelichnus* Ichnofacies (e.g. Kozur et al., 1994). Post-Paleozoic examples record also common elements of the *Chelichnus* Ichnofacies as dinosaur footprints of non-avian theropods of different sizes (*Grallator*, *Anchisauripus*, and *Eubrontes*), prosauropods (*Otozoum*), and ornithischians (*Anomoepus*) (e.g. Lockley and Hunt, 1995; Lockley et al., 1998). During the Cenozoic, numerous playa lake ichnofaunas consist of footprints produced by birds (e.g. Phoenicopteriformes Charadriiformes, Anseriformes, Passeriform) and are highly controlled by lake and pool salinity conditions; they can be associated with scarce

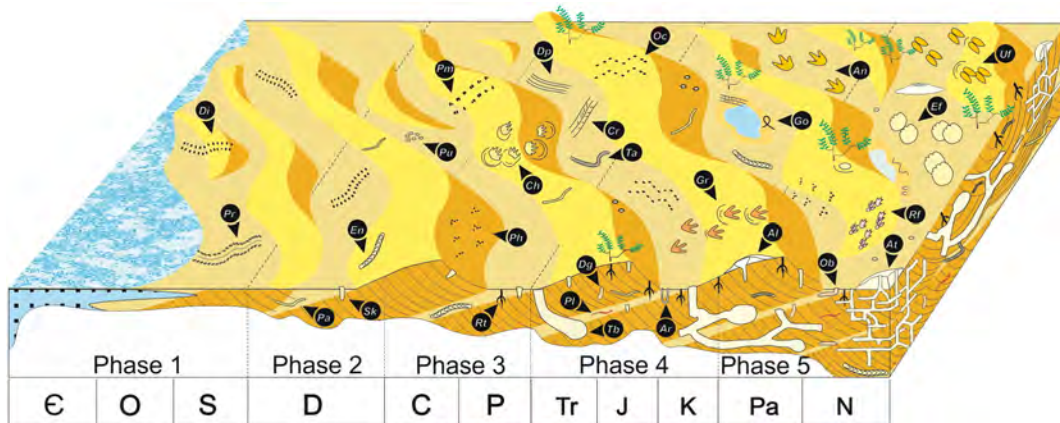
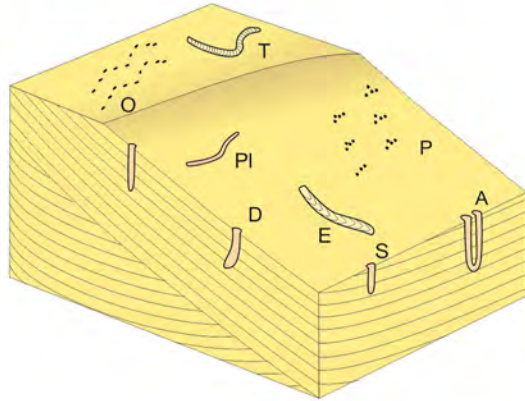


Fig. 18. Desert megatrends. See text for explanation.

Octopodichnus-Entradichnus Ichnofacies



Chelichnus Ichnofacies

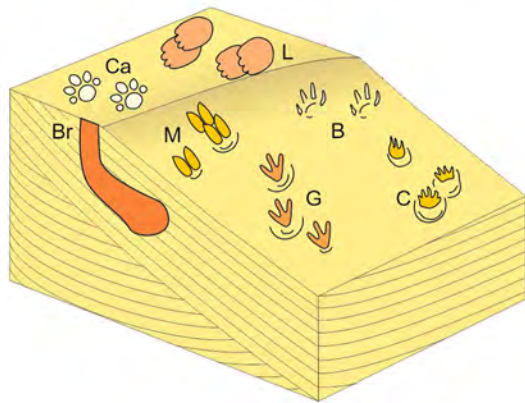


Fig. 19. Desert Ichnofacies. See text for explanation.

mammal footprints (e.g. Alonso, 1987; Leonardi, 1994; Melchor et al., 2012a).

6.4. Lake margin and overbanks

In arid deserts, most fluvial systems have an ephemeral nature. The high intensity and brevity of the flooding events, together with the scarcity of vegetation cover on the unconsolidated sandy substrates, determine their unconfined nature (Mountney, 2004). In semiarid climates, fluvial systems carry a significant input of water and sediment to the lake, where deltaic systems can develop (Mountney, 2004). Toward the center of the basin the water table is closer to the surface, favoring the growth of vegetation, more intense bioturbation, and the preservation of invertebrate and tetrapod footprints in the fluvial plains, the lake margins, and desert margins.

Numerous tetrapod burrows are documented on lake margins and fluvial overbanks facies in Permian and Triassic successions deposited under arid–semiarid climatic conditions with marked seasonality (Figs. 21, 22) (e.g. Colombi et al., 2008; Damiani et al., 2003; Dentzien-Dias, 2010; Groenewald et al., 2001; Krapovickas et al., 2013; Miller et al., 2001; Smith and Botha, 2005; Smith and Swart, 2002; Smith, 1987; Voigt et al., 2011). The vast majority of the Permian and Triassic burrows were interpreted as produced by synapsids, particularly cynodonts and dicinodonts (e.g. Damiani et al., 2003; Groenewald et al., 2001; Krapovickas et al., 2013; Smith, 1987). Also commonly recorded are Miocene to Pleistocene burrows which are related to the activity of mammals, specially rodents (e.g. Gobetz, 2006; Voorhies, 1975).

The footprints produced by shorebirds are commonly recorded in environmental settings developed under semiarid–arid climates, particularly from the Late Cretaceous onwards (e.g. Alonso, 1987; Contreras, 2006, 1996; de Gibert and Sáez, 2009; Doyle et al., 2000; Houck and Lockley, 2006; Kim et al., 2006; Mustoe, 2002; Tauber et al., 2007; Zhang et al., 2006). They are mostly present in fluvial-lacustrine and marginal marine settings, such as ephemeral fluvial channels, abandoned channels, temporary water bodies in overbanks, lake margins,

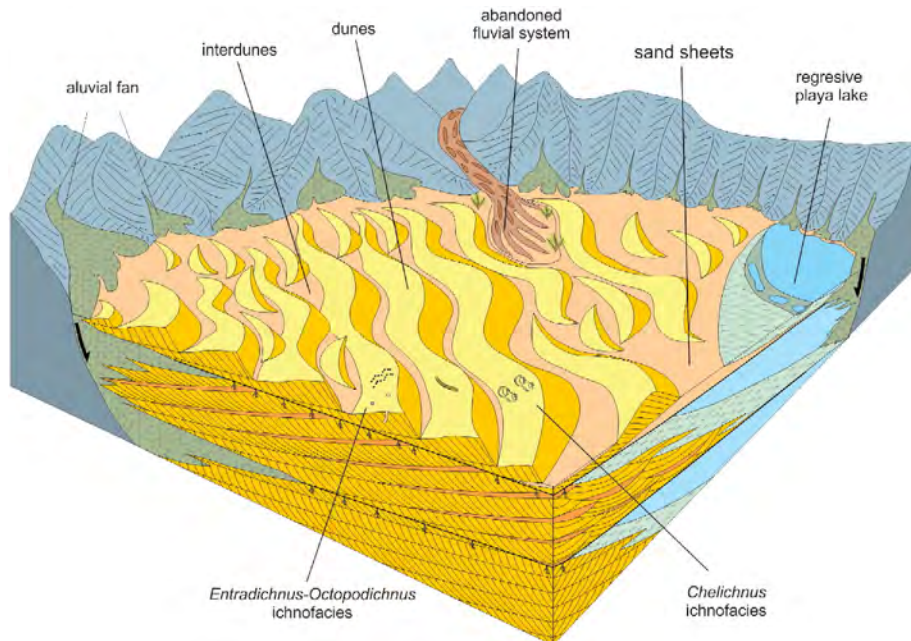


Fig. 20. Hyper-arid desert ichnology. Block diagrams taken from Mountney (2004).

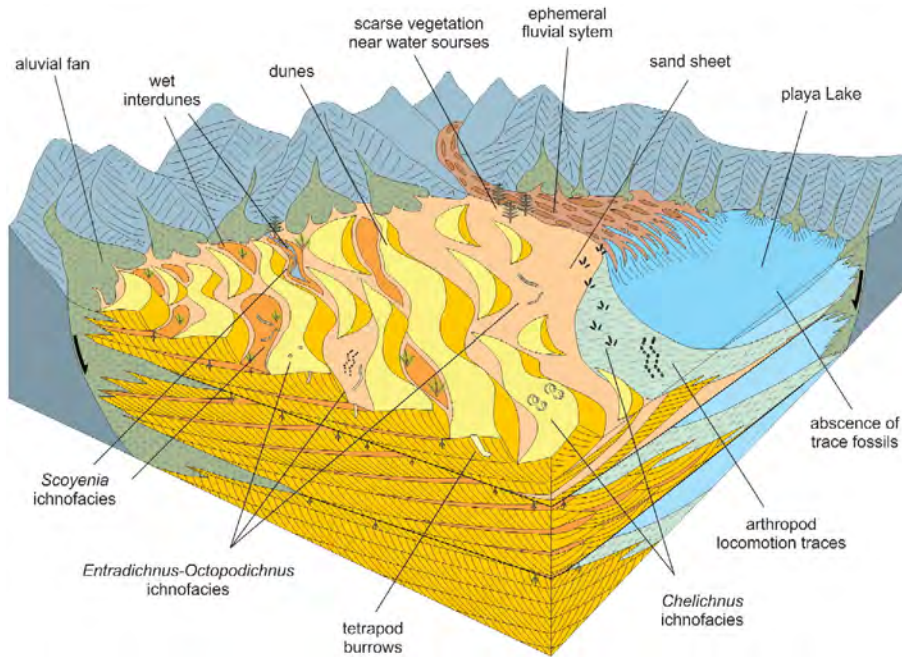


Fig. 21. Arid desert ichnology. Block diagrams taken from Mountney (2004).

river margins, evaporitic lakes and playas, soils, and lagoons (Fig. 22). Notably, shorebird footprints are significantly more common than other bird tracks, such as perching birds, large cursorial birds, and raptors (Doyle et al., 2000).

The invertebrate trace fossils recorded in lake margins and fluvial overbanks illustrate the *Scoyenia* Ichnofacies, at least in post-Paleozoic examples (Fig. 22). These are low energy settings episodically exposed to subaqueous and subaerial conditions; structures are produced by mobile detritus feeders that left behind horizontal traces (e.g. *Scoyenia*, *Taenidium*), locomotion traces – both trackways (e.g. *Diplichnites*) and trails (e.g. *Cruziana*) – and vertical dwelling structures (e.g. *Skolithos*).

During the Paleozoic, the ichnoassemblages of fluvial overbanks and lake-margin settings developed in deserts are composed exclusively by arthropod locomotion trace fossils.

The *Chelichnus* Ichnofacies is not present in these sub-environments and seems to occur only in those settings with stronger eolian influence. Tetrapod footprints preserved in lake margins and overbank deposits are the most diverse and, as it might be expected, differ significantly between Paleozoic, Mesozoic, and Cenozoic examples. Their putative inclusion into any tetrapod Ichnofacies seem speculative at most, since the ichnofacies model proposed by Hunt and Lucas (2007a) has not been yet fully validated (see Krapovickas, 2010).

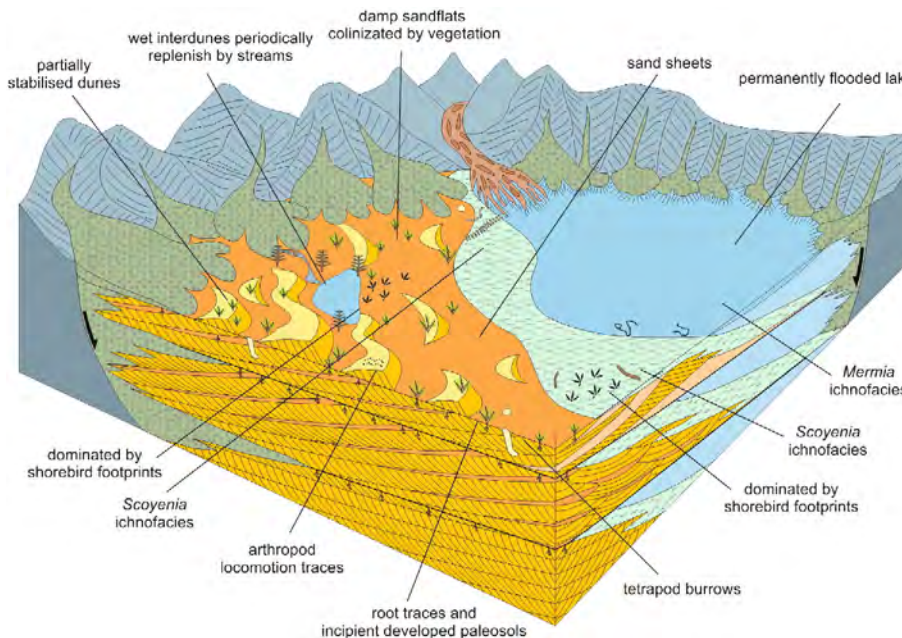


Fig. 22. Semi-arid desert ichnology. Block diagrams taken from Mountney (2004).

7. Desert systems, climate change, and trace fossils

Deserts currently occupy about one third of the land surface, in areas where the rate of evapotranspiration exceeds precipitation for most of the year (e.g. Buol et al., 1997). Accordingly, the interaction of precipitation and nutrient availability is critical in controlling desert community dynamics and ecology (Whitford, 2002). Additionally, episodic depositional events, such as flashfloods and windstorms, have significant impact in desert ecosystems (Mountney, 2006, 2004). The inhabitants of deserts have a number of behavioral and/or physiological adaptive traits allowing them to deal with adverse temperature and water balance conditions. Furthermore, favorable microclimate occupation is essential for surviving in these settings (Whitford, 2002). Current ideas accounting for desert system dynamics in response to regional climate are developed in a series of conceptual models (Mountney, 2006, 2004). These dynamic models describe deserts as determined by intrinsic sedimentary behavior (e.g. dune migration) and constrained by external forces, such as climate. In these models, a variety of landscape units (eolian sand seas, salt flat and playa lake systems, ephemeral rivers and alluvial fans) interact in response to regional-scale climate variations in hyper-arid, arid, and semiarid climatic settings (Mountney, 2006, 2004).

In hyper-arid climatic settings, the regional water table falls well below the accumulation surface in most desert regions. Accumulation occurs as a consequence of downwind deceleration in wind strength, and is largely composed of extensive dune systems (Mountney, 2006, 2004). The associated interdune areas, reduced to isolated depressions, are exposed to accelerated airflows and subject to intense erosion. Consequently, dunes grow and expand at expenses of interdune flat areas (Mountney, 2006, 2004). Ancient deserts completely developed under hyper-arid climatic conditions rarely preserve trace fossils due to the absence of moisture near the surface (Buatois and Mángano, 2011). However, locally and/or temporally, wet and partially stabilized levels may occur occasionally in predominantly dry successions (Mountney, 2006). These wet periods enable the development of life and thus, preservation of biogenic structures in deserts. Either in hyper-arid or arid deserts, trace fossils are mostly preserved in wet eolian settings. Nonetheless, some classic examples of predominantly dry eolian systems, such as the Jurassic Navajo and Wingate formations of USA, as well as the Cretaceous Botucatu Formation of Brazil, preserve biogenic structures of the *Octopodichnus*–*Entradichnus* and the *Chelichnus* Ichnofacies during periods of both dry and wet conditions (Fig. 20) (Ekdale et al., 2007; Fernandes and De Souza Carvalho, 2008; Leonardi, 1994; Lockley and Hunt, 1995; Lockley et al., 1998; Loope, 2006b; Milàn and Loope, 2007; Rainforth, 2001; Seiler and Chan, 2008).

In arid deserts, wet eolian systems are dominant. The water table, or its capillary fringe, is in contact with the accumulation surface and wet sand limits the sediment availability for transport (Mountney, 2004). Importantly, wet eolian systems will likely afford greater opportunity for preservation of traces. The Jurassic Entrada Sandstone, a classic example of a wet eolian system, was one of the examples on which the *Entradichnus* Ichnofacies was proposed by Ekdale et al. (2007). Although wet eolian systems are less widely recorded than dry systems, they alternate in arid deserts and most of the desert ichnofaunas identified in the fossil record are considered part of arid deserts with alternating dry and wet periods (Mountney, 2006, 2004). Arid deserts present complex patterns of dunes combined with dry, wet, and flooded interdunes. Dry desert elements, such as dunes, interdunes and sand sheets, are characterized by the classical desert trace fossils ascribed to the *Entradichnus*–*Octopodichnus* and *Chelichnus* Ichnofacies (Fig. 21). Slight rises in regional precipitation result in elevation of the water table and increase in fluvial discharge into desert-margin areas that provide water and sediment to the system (Mountney, 2004). These factors result in local concentration of trace fossils in wet interdunes and ephemeral fluvial systems that mostly correspond to the *Scoyenia* and *Chelichnus* Ichnofacies (Fig. 21). Stabilized areas may occur (e.g.

vegetated areas, surface crust), allowing the local development of roots and the accumulation of sands (Mountney, 2006). In playa lake margins, arthropod locomotion traces and the vertebrate footprints of the *Chelichnus* Ichnofacies are formed during regressive phases, whereas traces fossils ascribed to the *Scoyenia* and *Chelichnus* Ichnofacies are formed during transgressive phases.

Regional climatic variations involving the rise of water and sediment input into deserts, by major magnitude and frequency of rainfall, flash flood, and the establishment of major hydrological systems, cause the shifting from arid to semiarid deserts (Mountney, 2004). As such, the water table is high and a large part of the desert is stabilized in semiarid deserts. Playa lakes expand by the addition of freshwater and become freshwater lakes. On lake margins and fluvial overbanks sub-superficial horizontal feeding and vertical dwelling trace fossils dominate, as well as superficial locomotion traces ascribed to the *Scoyenia* Ichnofacies (Fig. 22). This is mostly true for Mesozoic and Cenozoic ichnoassemblages, whereas Paleozoic ichnoassemblages are mostly composed by superficial locomotion traces. In contrast, tetrapod ichnofaunas are dominated by shorebird footprints on lake margins and small temporary water bodies. Fluvial overbank settings preserve a wider variety of tetrapod tracks and trackways that could be linked to a variety of tetrapod ichnofacies, but not the *Chelichnus* Ichnofacies. The vegetation and surface cementation play a major role in accumulation, restricting sediment availability (Mountney, 2006). Root traces may be abundant in stabilized sands and incipient paleosols develop. Finally, tetrapod burrows are commonly recorded in semiarid overbanks (Krapovickas et al., 2013).

8. Summary

A systematic review of all the available information about vertebrate and invertebrate trace fossil preserved in desert successions suggests that deserts were by far more diverse and complex than has previously been acknowledged. By the elaboration of a comprehensive database that summarizes all life known in eolian deposits from the Cambrian to the Recent, we propose a summary of colonization trends and evolutionary turnovers in deserts, we reviewed the ichnofacies models proposed for deserts and, integrated them into more comprehensive dynamic desert models attending to climate change. Below we summarize the most significant conclusions arising from this study.

The colonization trends and evolutionary turnovers displayed by eolian ichnofaunas are summarized in five phases of desert colonization: (1) incursions into coastal deserts (Cambrian–Silurian). It coincides with the initial phases of terrestrialization during the early Paleozoic and involves incursions by nearshore amphibious arthropods, such as euhycarionids, eurypterids, scorpions, and myriapods. (2) Dune pioneers (Devonian), mostly arthropod incursions and colonization of inland deserts from other terrestrial, mostly fluvial, habitats. Among the earliest true inland desert inhabitants were stem-group arachnids or arachnids, together with myriapods. (3) Tetrapod colonization of sand seas (Carboniferous–Permian). By the Early Permian tetrapods were present in desert on a global scale and the dominant group was most likely the synapsids. (4) Major desert infaunalization (Triassic–Cretaceous), due to the increase of sub-superficial activity of holometabolous insects, such as beetles and hymenopterans, and arachnids, (5) establishment of modern desert communities (Paleogene–Recent), with the highest levels of animal activity – by bioturbation indexes – and more diverse behaviors recorded.

Both invertebrate (*Octopodichnus*–*Entradichnus*) and tetrapod (*Chelichnus*) ichnofacies models for deserts are herein reviewed, formally organized and, the environmental parameters in which they occur proposed: both ichnofacies occur in mobile and temporary stabilized sandy substrates, subject to frequent erosion and deposition, to strong seasonality and, to reduced humidity and nutrient availability.

Desert trace-fossil distribution can be understood as reflecting the partitioning of desert settings in a mosaic of landscape units,

characterized by water content and its temporal fluctuations, nutrient availability, nature of the substrate, and the dominant organisms present. Eolian dunes, interdunes, and sand sheets mostly host sub-superficial dwelling trace fossils and surficial locomotion traces ascribed to the *Octopodichnus*–*Entradichnus* Ichnofacies and tetrapod footprints and burrows ascribed to the *Chelichnus* Ichnofacies. As the previous case, wet interdunes record the *Chelichnus* Ichnofacies but differ in documenting the *Scoyenia* Ichnofacies for invertebrates. Playa-lake deposits contain almost exclusively surficial arthropod locomotion trace fossils during regressive phases and poor examples of the *Scoyenia* Ichnofacies during transgressive phases, but still record the *Chelichnus* Ichnofacies. The invertebrate trace fossils recorded in lake margins and fluvial overbank areas illustrate the *Scoyenia* Ichnofacies. The *Chelichnus* Ichnofacies is not present in these sub-environments and seems to occur only in those settings with stronger eolian influence.

The landscape units interact in response to regional climate and fluctuate within hyper-arid, arid, and semiarid climatic settings. Deserts completely developed under hyper-arid climatic conditions rarely preserve trace fossils due to the absence of moisture near the surface. However, the alternation of wet periods may allow the development of life and thus preserve biogenic structures of the *Octopodichnus*–*Entradichnus* and the *Chelichnus* Ichnofacies. In arid deserts the water table, or its capillary fringe, is in contact with the accumulation surface and wet sand limits the sediment availability for transport. Dry desert elements (e.g. dunes, interdunes, sand sheets) typically record the *Entradichnus*–*Octopodichnus* and *Chelichnus* Ichnofacies, whereas wet desert elements (e.g. wet interdunes, ephemeral fluvial systems) illustrate the *Scoyenia* and *Chelichnus* Ichnofacies. In semiarid systems playa lakes expand by the addition of freshwater, evolving into freshwater lakes and fluvial systems may become more common. Lake margins and fluvial overbanks typically contain trace-fossil assemblages that may be ascribed to the *Scoyenia* Ichnofacies and tetrapod burrows are commonly recorded in fluvial overbank settings.

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