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COMPLEX TETRAPOD BURROWS FROM MIDDLE TRIASSIC RED BEDS OF THE ARGANA BASIN (WESTERN HIGH ATLAS, MOROCCO)

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ABSTRACT

Although burrowing ability has been widespread in tetrapods for more than 300 million years, subsurface dwelling structures that indicate communal behavior are poorly evidenced from pre-Cenozoic strata. Here we present recently discovered tetrapod burrows from Middle Triassic red beds of the Argana Basin in central Morocco, whose complexity suggests an origin by gregarious animals. The well-preserved burrows occur in interbedded mudstones and sandstones interpreted as channel and overbank deposits of ephemeral, braided streams. All burrows originate from the top of thick-bedded sandstones and descend as moderately inclined (10°–30°), partially spiral tunnels to laterally extended, branched chambers in underlying mudstones. Tunnel segments are biconvex to planoconvex in cross section, up to 20 cm wide and 12 cm in maximum height and exhibit transverse scratch marks along the ceilings and sidewalls. Distinctive burrow characteristics include a laterally sinuous geometry (wavelength λ = 38–45 cm; amplitude A = 5–10 cm) of the tubelike passages and the presence of grouped alcoves in terminal chambers. We attribute the burrows to procolophonids or therapsids based on closely associated tetrapod tracks and the limited diameter of the excavations. Our findings represent the second oldest record of communal fossorial behavior by tetrapods and the oldest example from low-latitude areas. Beyond providing refuge from predators, these elaborate underground structures probably functioned as a buffer against diurnal or seasonal variations of air temperature and humidity in a semiarid habitat that was situated just north of the paleoequator.

INTRODUCTION

Recent advances in vertebrate paleontology suggest that fossorial behavior in tetrapods evolved long before the Cenozoic in a variety of groups, including temnospondyls (Storm et al., 2010), lysorophids (Hasiotis et al., 1993; Hembree et al., 2004, 2005), therapsids (Smith, 1987; Groenewald et al., 2001; Damiani et al., 2003; Lucas et al., 2006; Colombi et al., 2008; Tanner and Lucas, 2008; Modesto and Botha-Brink, 2010; Bordy et al., 2011; Riese et al., 2011), mammals (Hasiotis, 2004; Hasiotis et al., 2004; Luo and Wible, 2005; Simpson et al., 2010; Riese et al., 2011), procolophonids (Stanistreet and Turner, 1979; Groenewald, 1991; deBraga, 2003; Sidor et al., 2008), and dinosaurs (Varrichio et al., 2007; Martin, 2009; Huh et al., 2010). Related burrow architecture ranges from simple tubes (Hembree et al., 2004, 2005) and gently dipping, distally enlarged tunnels (Loope, 2006; Varrichio et al., 2007; Martin, 2009; Modesto and Botha-Brink, 2010; Storm et al., 2010; Bordy et al., 2011), to helical, single-chamber structures (Smith, 1987; Miller et al., 2001) and networks of multiple branched tunnels and chambers (Groenewald et al., 2001; Hasiotis et al., 2004; Lucas et al., 2006; Colombi et al., 2008; Riese et al., 2011). Complex tetrapod burrow systems that indicate communal behavior by the producers are poorly known from pre-Cenozoic strata including only six published occurrences: (1) The earliest evidence of colonial dwellings comes from the Upper Triassic Driekoppen Formation of the Karoo Basin, South Africa and is attributed to therapsids (Groenewald et al., 2001); (2–4) similar complex burrows equally referred to advanced synapsids are reported from the Late Triassic Chinle Formation of southeastern Utah, United States (Hasiotis et al., 2004), the Late Triassic Ischigualasto Formation of northwestern Argentina (Colombi et al., 2008), and the Lower Jurassic Navajo Sandstone of east-central Utah, United States (Lucas et al., 2006; Riese et al., 2011); (5) large-diameter burrow networks possibly constructed by fossorial mammals are recorded from the Upper Jurassic Morrison Formation of southern Utah, United States (Hasiotis, 2004; Hasiotis et al., 2004); (6) finally, mammalian den complexes probably excavated and used by multiple individuals were mentioned from the Upper Cretaceous Wahweap Formation of southern Utah, United States (Simpson et al., 2010). The Late Triassic origin of recently published tetrapod burrow complexes from the Holy Cross Mountains in Poland (Tałanda et al., 2011) is questioned given their preservation in pedogenically overprinted mudstones close to the present-day ground surface.

Here we describe an occurrence of burrows from Middle Triassic red beds of the Argana Basin in central Morocco that was discovered by one of us (JWS) during a joint Moroccan-German field campaign in March 2008. Detailed analyses of the ichnofossils and the fossil-bearing strata undertaken in May 2009 and February 2010 revealed a uniquely abundant and well-preserved record of subterranean tetrapod activity. The areal extent and complexity of the terminal chambers strongly suggests construction and use of these burrows by gregarious animals. If this is the case, the recent findings represent the second oldest record of communal fossorial behavior by tetrapods and the earliest example from low-latitude areas. This paper focuses on a detailed description of the Moroccan ichnofossils and their sedimentological context in order to evaluate the paleobiological and paleoenvironmental significance of these traces.

MATERIAL AND METHODS

Our study is based on 68 fossil burrow segments including parts of entrances, tunnels, and chambers that have mainly been observed in place (~85%) or, less frequently, on loose sandstone boulders (~15%). The majority of the material comes from a single locality on top of an up to 40-m-high cliff section, where the burrow-bearing horizon of interbedded fluvial sandstone and muddy siltstone is laterally exposed for about 120 m. Ninety percent of the recorded burrow segments at this locality represent tunnels, whereas evidence for entrances and chambers is comparatively rare. The analysis of the trace fossils was largely carried out in the field due to their preservation within uncollectable thick-bedded sandstone. All burrow segments were

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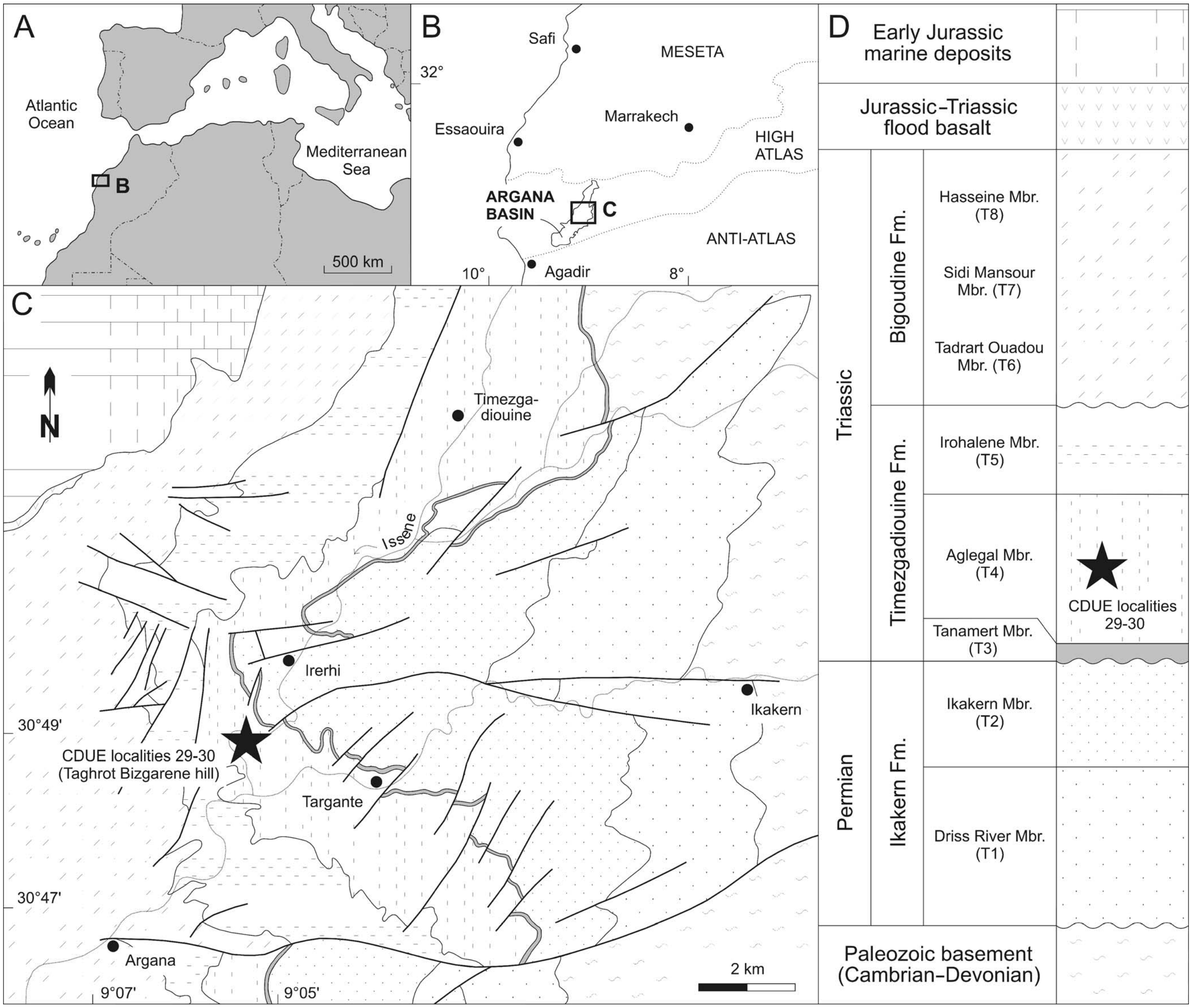


FIGURE 1—Location and geological overview of the study area. A–B) Position of the Argana Basin in northwestern Africa and central Morocco. C–D) Simplified geological map (after Tixeront, 1974) and generalized lithostratigraphic subdivision of the Paleozoic-Mesozoic volcano-sedimentary succession in the central part of the Argana Basin. The asterisk indicates the position of described tetrapod burrows (CDUE localities 29–30).

consecutively numbered, described in detail, measured, drawn to scale, and photographed. In order to record the sedimentological context of the fossils as accurately as possible we measured 15 detailed stratigraphic sections along the most prolific part of the burrow-bearing horizon at 5-m-spaced intervals. Thin sections of selected burrow fill and enclosing sediment were produced to support the petrographic analysis carried out in the field.

No specimens could be collected due to the large size and mainly *in situ* position of the trace fossils. Locality data are archived at the Department of Earth Sciences, Chouaïb Doukkali University, El Jadida, Morocco (CDUE).

LOCALITY AND DEPOSITIONAL ENVIRONMENT

All fossils described come from the Argana Basin between Marrakech and Agadir in southern central Morocco (Fig. 1). The Argana Basin refers to an approximately 20-km-wide and 70-km-long, NNE-SSW trending area of well-exposed Permo-Triassic red beds along the western margin of the High Atlas mountain range. The 2,500–5,000-m-thick, predominantly siliciclastic succession consists of alluvial, fluvial, lacustrine, eolian, and playa deposits that accumulated in a continental rift basin during the initial opening phase of the central Atlantic (Manspeizer, 1988; Zühlke et al., 2004).

Tixeront (1974) proposed a subdivision of the Argana Basin red bed succession into eight lithostratigraphical units (T1–T8), which Brown (1980) formally assigned to three formations (Fig. 1). These are, from base to top, the Ikakern Formation (T1–T2; 900–1,800 m), the Timezgadiouine Formation (T3–T5; 1000–2000 m), and the Bigoudine Formation (T6–T8; 300–1,500 m), with each of them being separated from older strata by either an angular or erosional unconformity. The basal Ikakern Formation consists of alluvial fan conglomerates (T1) grading vertically and laterally into alluvial plain conglomerates, sandstones, and mudstones (T2). The Timezgadiouine Formation is represented by coarse-grained braided river deposits (T3), playa mudstones with intercalations of sheetflood and ephemeral stream sandstones (T4), and alluvial plain sandstones and mudstones (T5). The Bigoudine Formation grades from braided river conglomerates and eolian sandstones (T6) at the base into increasingly fine-grained

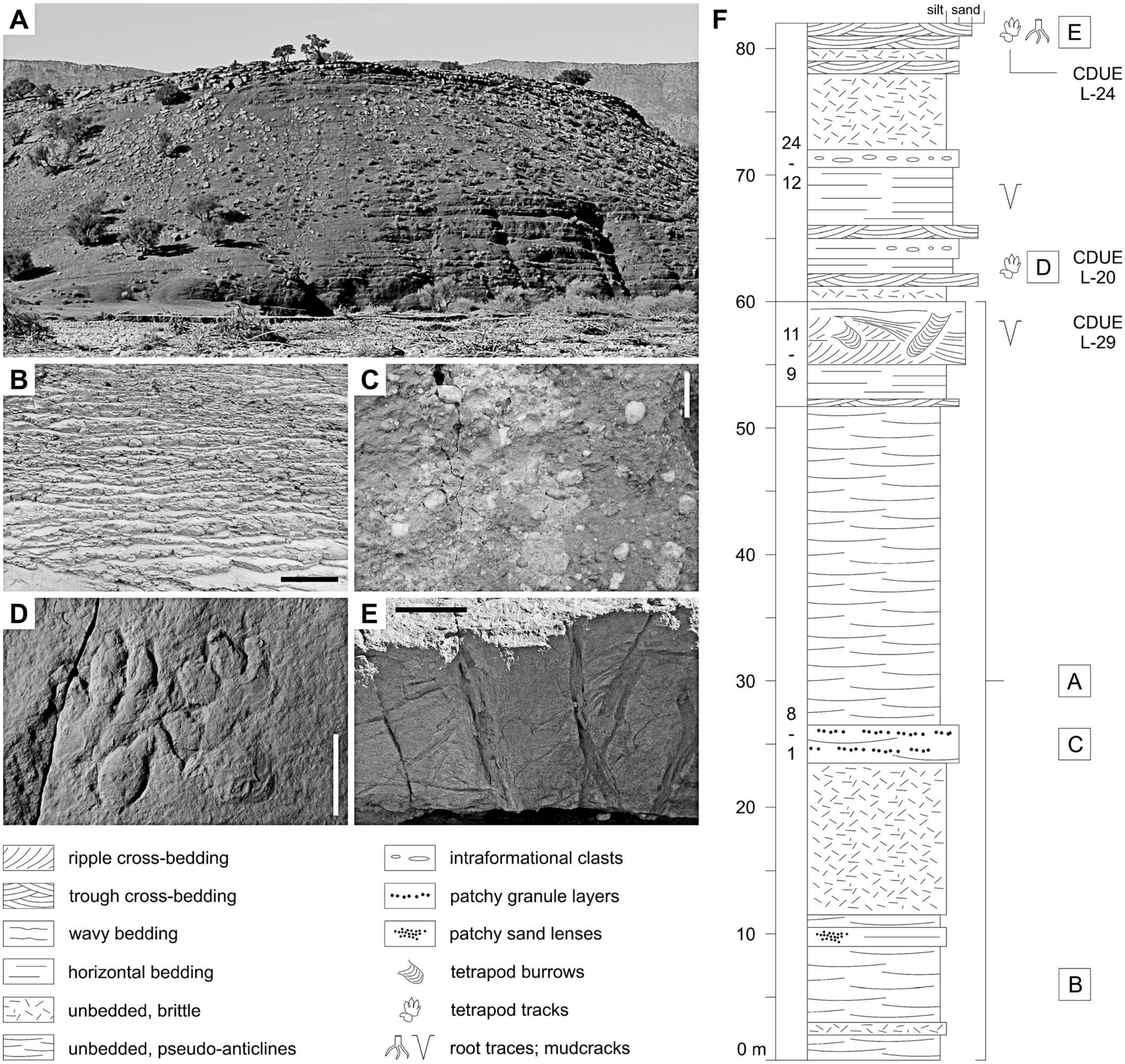


FIGURE 2—Geological setting at CDUE locality 29. A) Steep northwestern slope of Taghrot Bizgarene ridge. Distance from base to the top of the hill is ~40 m. B) Curviplanar surfaces (pseudo-anticlines) in pedogenic mudstones. C) Pebbly mudflow deposit. D) Convex pedal tracks of *Isochirotherium coureli* (Demathieu, 1970). E) Root traces in cross-bedded, fluvial sandstone. F) Taghrot Bizgarene stratigraphic section illustrating the position of the described tetrapod burrows and the phenomena highlighted in A–E. B, scale bar = 20 cm; C, scale bar = 1 cm; D, scale bar = 10 cm; E, scale bar = 5 cm.

partially evaporitic playa red beds (T7–T8) toward the top. The Permo-Triassic sedimentary succession of the Argana Basin is terminated by up to 150-m-thick tholeiitic basalts that unconformably overlie slightly deformed mudstones of the Bigoudine Formation.

The Timezgadiouine and Bigoudine formations are dated as Middle to Late Triassic (Ladinian to earliest Norian) based on vertebrate remains, tetrapod tracks, palynomorphs, and charophytes (Jalil, 1999; Tourani et al., 2000; Medina et al., 2001; Jalil et al., 2009; Klein et al., 2011). Recently discovered tetrapod footprints from the hitherto fossil-barren basal member of the Timezgadiouine Formation suggest, however, that sedimentation of the Mesozoic part of the Argana red beds started in the Early Triassic (Klein et al., 2010). Radiometric age determinations of tholeiitic basalts capping the succession range between 197.8 ± 0.7 and 201.7 ± 2.4 Ma (Hettangian to Rhaetian; Verati et al., 2007).

The burrows of this work were discovered in fluvial red beds on top of the northwest-southeast trending Taghrot Bizgarene hill at the left bank of the Oued Issene river about 2 km SSW of Irerhi (Figs. 1–2). The majority of studied traces are located at the northwestern end of the hill (CDUE locality 29; N30°49′06.1″ W009°05′23.1″), but similar burrows, though less abundant, have also been observed at the southeastern end of the ridge (CDUE locality 30; N30°48′49.1″ W009°05′00.3″). The Taghrot Bizgarene hill exposes on its steep northern face and the gently dipping southern slope an approximately 80-m-thick section of arid-zone fluvio-lacustrine red-beds that we refer to the middle part of the Aglegal Member (T4) of the Timezgadiouine Formation. Beginning at the base of the slope, the section is dominated for the first 52 m by reddish-brown siltstones (beds 1–8; Fig. 2). This monotonous series is mainly composed of two lithotypes: clayey siltstones that are pervasively structured by concave-upward, curvipla-

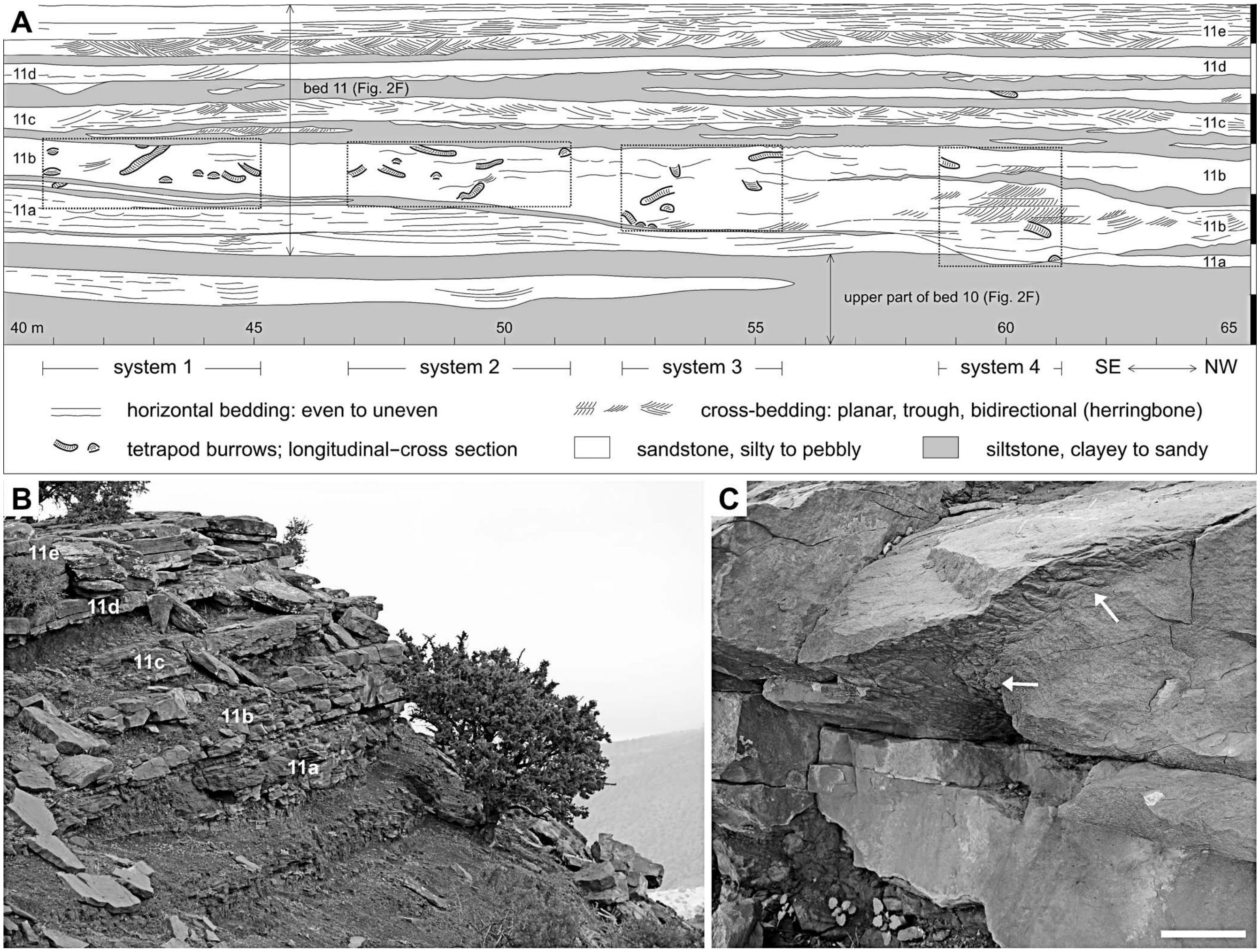


FIGURE 3—Tetrapod burrow-bearing horizon on top of the Taghrot Bizgarene hill (CDUE locality 29). A) Interpretative drawing of a 25-m-wide section illustrating intense bioturbation of sandstone bed 11b. Note clustering of the trace fossils. Both axes are equally scaled. B) Outcrop exposure at CDUE locality 29 showing the first 10 m of the section figured in A. Numbers correspond to the sandstone units in A; view is to the NW. The tree in the center is ~4 m tall. C) Close-up view of sandstone bed 11b with typical burrow section; arrows point to transverse grooves interpreted as scratch marks at the roof of a descending tunnel. Scale bar = 10 cm.

nar slickensided planes (pseudo-anticlines), and sandy siltstones easily recognizable by their massive appearance. Small aggregates (diameter ~1–3 mm) of needle-like gypsum or zeolite crystals may locally occur in both siltstone types. The most coarse-grained units of this part of the section are massive sandy siltstones to silty sandstones with matrix-supported granules that tend to weather out as resistant benches (beds 4, 7; Fig. 2).

The lithology notably changes 3–4 m below the burrow-bearing horizon by the intercalation of stratified silt and sandstones into the red mudstones (beds 9–10; Figs. 2–3). This zone passes upward into an approximately 5-m-thick unit of thick-bedded sandstones and siltstones containing abundant evidence of tetrapod burrowing activity (bed 11; Figs. 2–3). Five prominently weathered layers of sandstone (beds 11a–e; Fig. 3), ranging from 30 (bed 11d) to 230 cm (bed 11b) in maximum thickness, can be laterally traced for tens to hundreds of meters. Grain-size and color of these rocks varies from reddish-brown, silty fine-grained sandstone to light grayish-brown, pebbly coarse-grained sandstone. Volumetrically significant parts of the sandstones are of massive appearance, whereas subordinate stratified sections may show either horizontal bedding, small- to medium-scale planar, trough, or bidirectional cross-bedding, and, very locally, climbing ripples. Desiccation cracks are particularly common in beds 11b and 11c, whereas tetrapod footprints, indeterminate invertebrate burrows, ripple marks, and mud-pebble intraclasts have been rarely noticed throughout the unit. The individual sandstone beds rest with more or less irregular surfaces on dark reddish-brown, clayey to sandy, horizontally bedded siltstones whose maximum thickness ranges from 10 to 50 cm. Almost all tetrapod burrows at CDUE locality 29 occur in the thickest sandstone layer (bed 11b; Fig. 3).

At the southern slope of the Taghrot Bizgarene hill, the bioturbated sandstones and siltstones of beds 11a–e are overlain by a 22-m-thick succession of interbedded massive to stratified siltstones and generally cross-bedded sandstones (beds 12–24; Fig. 2). This part of the section is again dominated by red beds, but differs from the basal part by the frequent intercalation of intraformational conglomerates and pebbly sandstones, the presence of tetrapod footprints and root traces, as well as the absence of pseudo-anticlines.

The studied section at CDUE locality 29 can be subdivided into three generically similar parts: (1) The lower part is made up of weakly evaporitic, sandy playa mudflat deposits (beds 1–8; Fig. 2) whose clastic input was mainly derived from episodic sheet floods. Slickensided planes and homogenization of the dominant siltstones indicate extended periods of low or non-deposition that favored soil-forming processes, in particular shrinkage and swelling of expandable clays that now represent paleovertisols (Mack et al., 1993; Hofmann et al., 2000). These deposits, in conjunction with evaporites, signal arid climatic

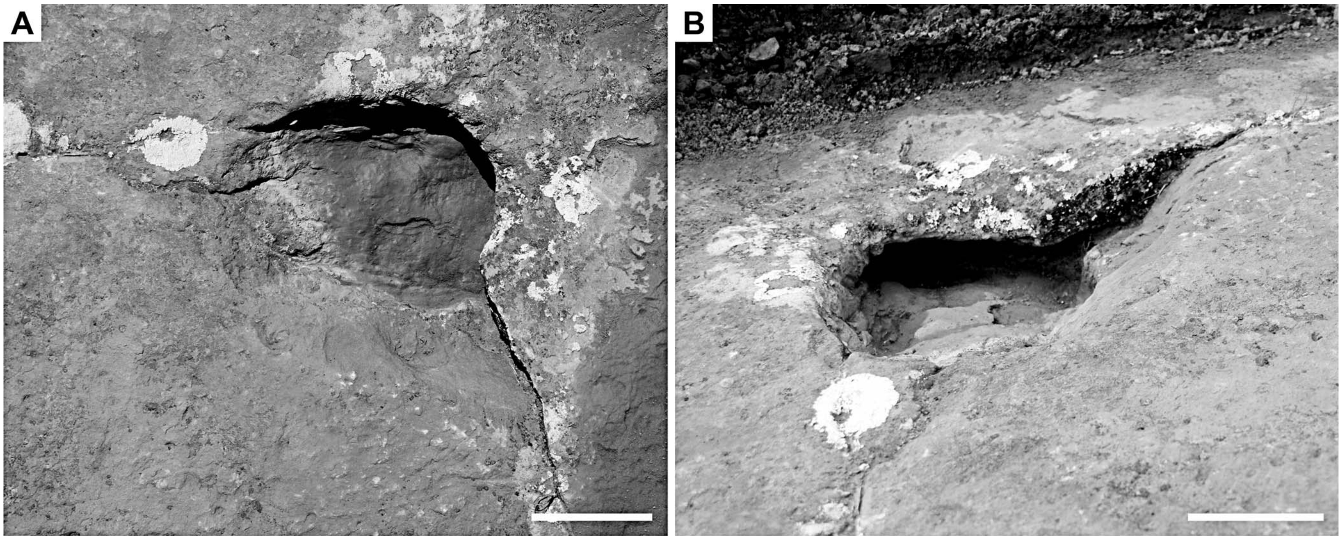


FIGURE 4—Surface-related burrow architecture. A–B) Oval-shaped depression on top of thick-bedded, fluvial sandstone at CDUE locality 30. Stratigraphic position and shallow inclination support interpretation as a burrow entrance. Same specimen seen from different angles. A–B, scale bar = 10 cm.

conditions with marked alternation of dry and wet periods. (2) Increasingly higher amounts of seasonal rainfall could account for the lithological change seen at the base of the upper third of the section (beds 9–11; Fig. 2). Well-developed interbedding of laterally extended, multistoried channel sandstones and overbank mudstones suggests deposition in an open plain with wide, braided streams. Mud-cracked surfaces and poorly sorted overbank fines indicate recurrent subaerial exposure and flooding events. (3) The uppermost part of the section (beds 12–24; Fig. 2) is the most heterogenic in terms of lithology and characterized by frequent interbedding of overbank mudstones and shallow, isolated channel sandstones. Fine-grained sediments are volumetrically dominant, pointing to decreased aggradation in a topographically low environment with braided-alluvial to floodplain deposition. Well-sorted fluvial sandstones, root traces, and a diverse tetrapod ichnofauna are evidence for at least seasonal availability of water, whereas mudcracks and abundant desiccation breccia suggest that long periods without precipitation occurred as well.

In summary, the sedimentary succession at CDUE locality 29 records a transition from an evaporitic playa mudflat to a braided-alluvial plain or floodplain that was probably caused by climatic shift from arid to semiarid conditions. Evidence of life is restricted to the upper part of the section with supposed higher amounts of seasonal rainfall. Nevertheless, climatic extremes, in particular recurrent droughts, likely represented a serious challenge for various terrestrial biota of this ancient dryland river habitat. With respect to the depositional environment, climatic conditions, and ecological constraints of the Triassic Argana ecosystem, the Cooper River valley of the Lake Eyre Basin, central Australia (Rust and Nanson, 1989; Hamilton et al., 2005), might be a good modern example for comparative analyses.

Abundant and well-preserved tetrapod footprints from CDUE locality 20 (bed 13; Fig. 2) and closely associated strata, assigned to the ichnotaxa *Chirotherium barthii*, *Isochirotherium coureli*, *Synaptichnium* isp., *Atreipus-Grallator*, *Rotodactylus* isp., *Rhynchosauroides* isp., and *Procolophonichnium* isp., suggest a Middle Triassic (Anisian-Ladinian) age for the burrow-bearing middle part of the Aglegal Member (Klein et al., 2011).

PALEOICHNOLOGY

The large-diameter burrows are interpreted to consist of three types of architectural elements: (1) entrances, (2) tunnels, and (3) terminal chambers. Each of these elements has a unique set of characters regarding shape, size, surficial morphology, stratigraphic position, and associated lithofacies type.

Entrances (Fig. 4)

Oval-shaped depressions on top of thick-bedded sandstones are interpreted as burrow entrances. Three of these structures were observed ranging from 14 to 18 cm in maximum width and 17 to 26 cm in maximum length. The depressions are gently sloped with an average inclination of 9°. Indistinct transverse grooves may be present on the steep sidewalls, whereas the bottom of the depression is always structureless. All burrows identified as entrances occur on the upper surface of 35–120-cm-thick, small-scale cross-bedded or uneven horizontally bedded, fine- to medium-grained sandstones.

Tunnels (Figs. 5–6)

Tunnel cross sections and longitudinal sections are the most commonly encountered parts of the burrows occurring at all levels within the bioturbated sandstone beds (Figs. 5A–D). The general architecture of the tunnels appears to be uniform, although there is some variety in form, size, and surficial morphology. Most tunnels are characterized by a planoconvex to flattened biconvex cross section (Fig. 5E). The maximum width of 24 analyzed cross sections ranges from 11 to 20 cm, whereas maximum height varies from 6 to 12 cm. Longitudinally cut tunnels, exposed for up to 115 cm in length, are moderately inclined (10°–30°) and descend in meter-wide, unpredictable turns (Figs. 5A–B). Systematic variation of burrow height in longitudinal tunnel sections is common (Figs. 5C–D), resulting from small-scale lateral sinuosity with wavelengths between 38 and 45 cm and amplitudes between 5 and 10 cm. A single specimen (Fig. 5F) documents a Y-junction with a bifurcation angle of 65°.

Walls and ceilings of open tunnels often exhibit distinct transverse grooves (Figs. 5E–F, 6) which are usually curved, up to 7 cm long, 0.1–0.3 cm deep, and spaced 0.6–1.3 cm apart (Figs. 5F, 6A–B). The radius of curvature ranges from 4 to 6 cm. In some cases, grooves on the tunnel roof appear to be serially aligned, forming a left and a right row (Fig. 6B). Curved transverse grooves on inclined ceilings always point convex side downward. Partial crossing of grooves is very common, resulting in comb-shaped textures on weathered surfaces (Figs. 5F, 6C). Wherever visible and identifiable as such, the tunnel floor is smooth (Fig. 6D). Tunnels occur in up to 150-cm-thick, cross-bedded to

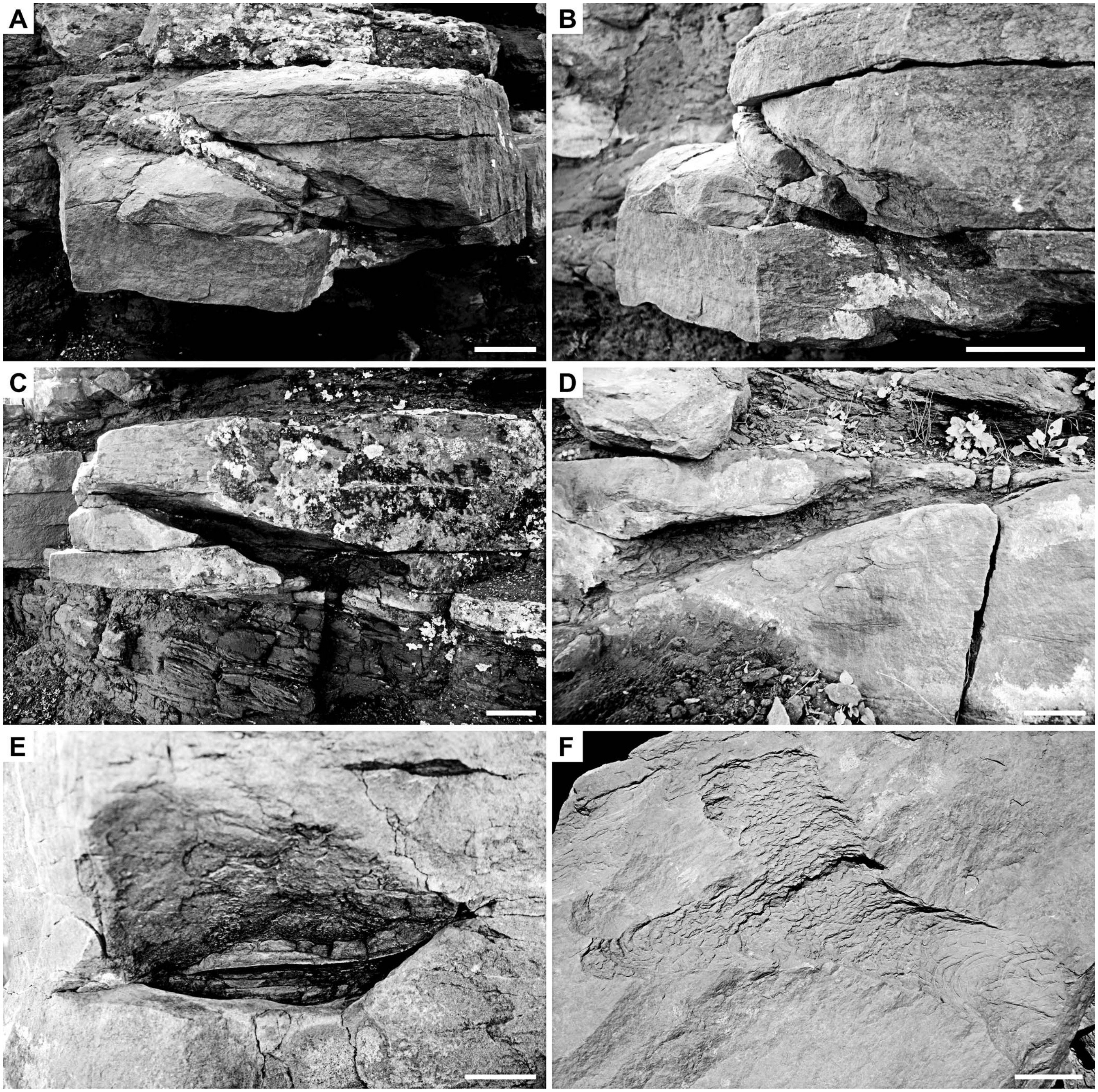


FIGURE 5—Tunnel architecture. A–B) Wide turn of a moderately inclined burrow segment, preserved in sandstone leading to underlying mudstone. Same specimen seen from different angles. C–D) Descending tunnels in sandstone showing rhythmical variation of burrow height due to lateral sinuosity. General broadening to the base is caused by a superimposed wide turn that is dextral in C, and sinistral in D. E) Flattened biconvex tunnel cross section; burrow filled with laminated sandy mudstone. F) Y-branched tunnel segment on fallen sandstone boulder. Note decreasing inclination of the burrow from the unbranched to the branched part and variable preservation of the transverse scratch marks. All specimens come from CDUE locality 29. A–E, scale bar = 10 cm; F, scale bar = 5 cm.

apparently massive fine-grained to medium-grained sandstones. Burrow fills are reddish-brown sandy mudstones often showing horizontal bedding. Up to six discrete layers have been recorded infilling a single tunnel segment (Fig. 5E).

Terminal Chambers (Fig. 7)

Two specimens with extended sets of transverse grooves on the lower surface of thick-bedded, fine- to medium-grained sandstone are interpreted to represent the roof of terminal chambers. Burrow fillings are not preserved. The naturally exposed structures are notable for their areal extent, large diameter, bedding-plane parallel orientation, and the presence of burrow enlargements and abundant blind tunnels. The first specimen (Fig. 7A) is a 45-cm-long excavation terminating into three alcoves (short blind burrows; 14–20 cm long, 13–18 cm wide) that meet at right angles. At the open side, the structure shows on an inclined plane the same pattern of convex downward grooves as being typical for tunnel ceilings.

A more complex terminus is represented by the second specimen (Figs. 7B–D). In this structure, which is extended over an area of ~1.5 m^2, two separate chambers are connected by a system of descending tunnels. The relatively short chamber to the left (Figs. 7B–C) terminates

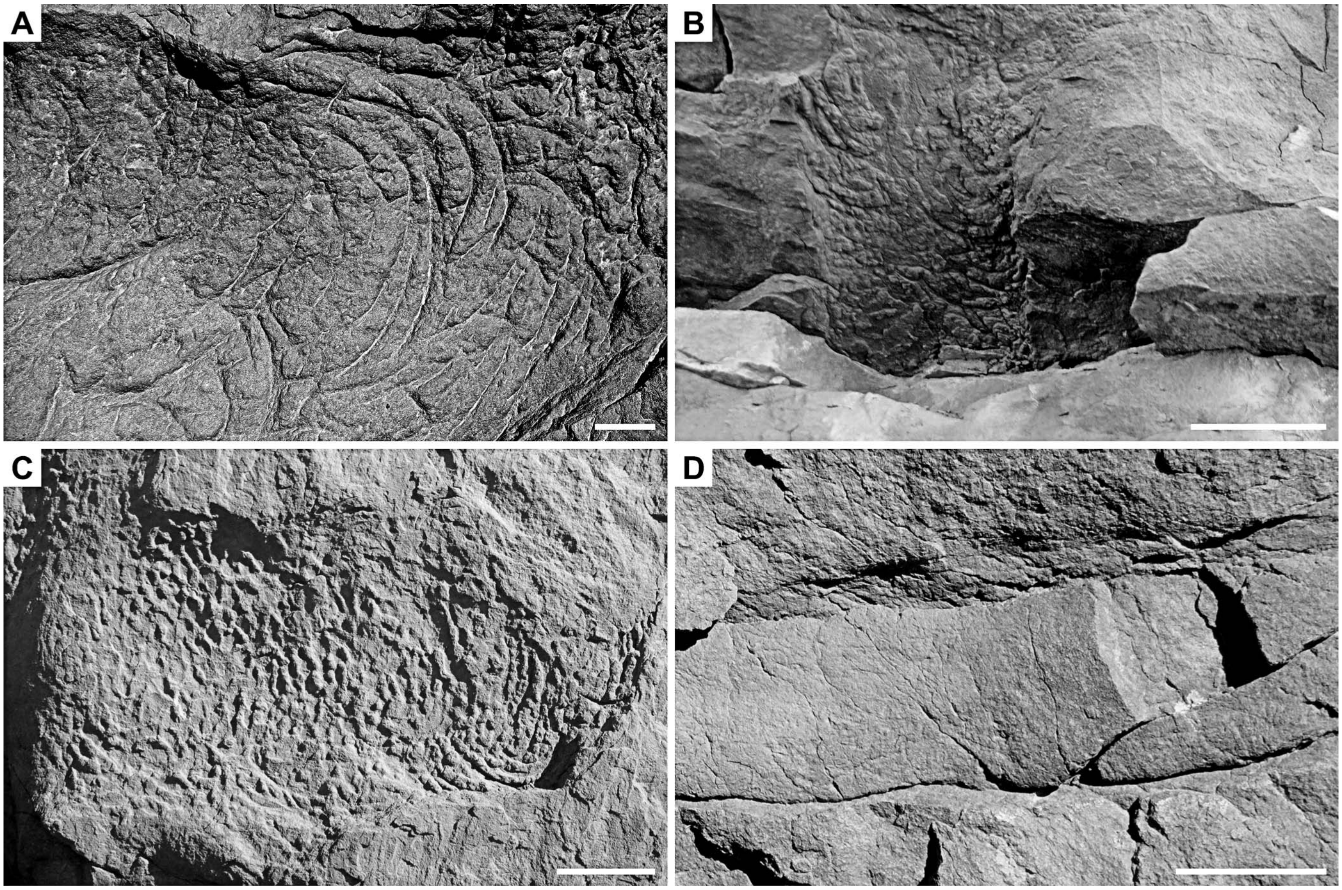


FIGURE 6—Surficial tunnel morphology. A–B) Transverse grooves interpreted as scratch marks preserved at the roof of open tunnels. The convex side of curved scratches always points downward in descending tunnels. C) Comb-shaped appearance of scratch marks on weathered surface. D) Smooth bottom side of filled tunnel; scratch marks of the mainly covered ceiling are visible along the margins of the burrow fill. All specimens are from CDUE locality 29. A, scale bar = 2 cm; B and D, scale bar = 10 cm; C, scale bar = 5 cm.

into two merged burrows of equal size. The more extended chamber to the right (Figs. 7B, D) consists of a proximal enlargement and two elongated blind tunnels diverging at an angle of ~120°.

DISCUSSION

Considering the complex architecture, large diameter, gently inclined entrances, sinuous tunnels, enlarged terminal chambers, and distinct transverse grooves, scratch-digging tetrapods are the most likely excavators of the described burrows (Groenewald et al., 2001; Miller et al., 2001; Hasiotis et al., 2004, 2007; Loope, 2006; Martin, 2009; Riese et al., 2011). Even though skeletal remains are not associated with these structures, careful comparative analyses of the burrow architecture, surficial morphology, and sedimentological context may be helpful to narrow the search for potential tracemakers and to interpret their behavior.

Burrow Architecture and Site Selection (Fig. 8; Table 1)

The most intensively bioturbated sandstone at CDUE locality 29 reveals a nonrandom distribution of *in situ* burrow sections that tend to form 2.5–4.5–m-wide and 1–3 m laterally spaced aggregations (bed 11b; Fig. 3). At least 12 concentrations of tetrapod burrows were identified along the outcrop. This type of clustering suggests that the burrow sections belong to discrete but complex systems. Each system is composed of entrances, tunnels, and terminal chambers. The entrance is the beginning of a descending tunnel and differs from deeper burrow parts by its low angle of inclination. Entrances represent <5% of the observed burrow segments at the Taghrot Bizgarene hill. This minor portion is probably an artifact because the upper part of the main bioturbated sandstone bed 11b is poorly exposed (Fig. 3B). For the following reasons we propose that there were at least two surface connections (e.g., entrance and exit; Fig. 8) for the individual burrow system: (1) sections of largely unbranched tunnels are too common and too closely spaced in most clusters to explain their distribution as a single tubelike passage making wide turns only; (2) the interconnected chambers of the more complex burrow terminus (Fig. 7B) suggests access by descending tunnels from two different directions.

The geometry of the tunnels with two superimposed types of sinuosity is one of the most distinctive features of the described burrows (Fig. 8). Although truly helical structures as reported for burrows of Late Permian dicynodonts (Smith, 1987) and Miocene beavers (Martin and Bennett, 1977) are absent, the Argana burrows share with them the regular sinuous tunnels. In comparison to simple straight tunnels, this design increases the burrow subsurface air volume and the burrow wall surface area—two values that have a positive effect on gaining a more consistent subsurface temperature and humidity (Meyer, 1999).

Branching seems to be restricted to tunnels in close proximity to terminal chambers (Fig. 5F) and intra-chamber burrow segments (Figs. 7B, 8). There is no evidence for branching in descending tunnels well above terminal chambers. All bifurcations are Y-shaped (Figs. 5F, 7B) and differ from T-junctions of similarly complex tetrapod burrows from the Early Triassic of the Karoo Basin (Groenewald et al., 2001).

Chambers are the most complex part of the described burrows comprising enlargements, secondarily branched tunnels, and blind tunnels of various length (Fig. 8). Dead-end excavations (Figs. 7A–B)

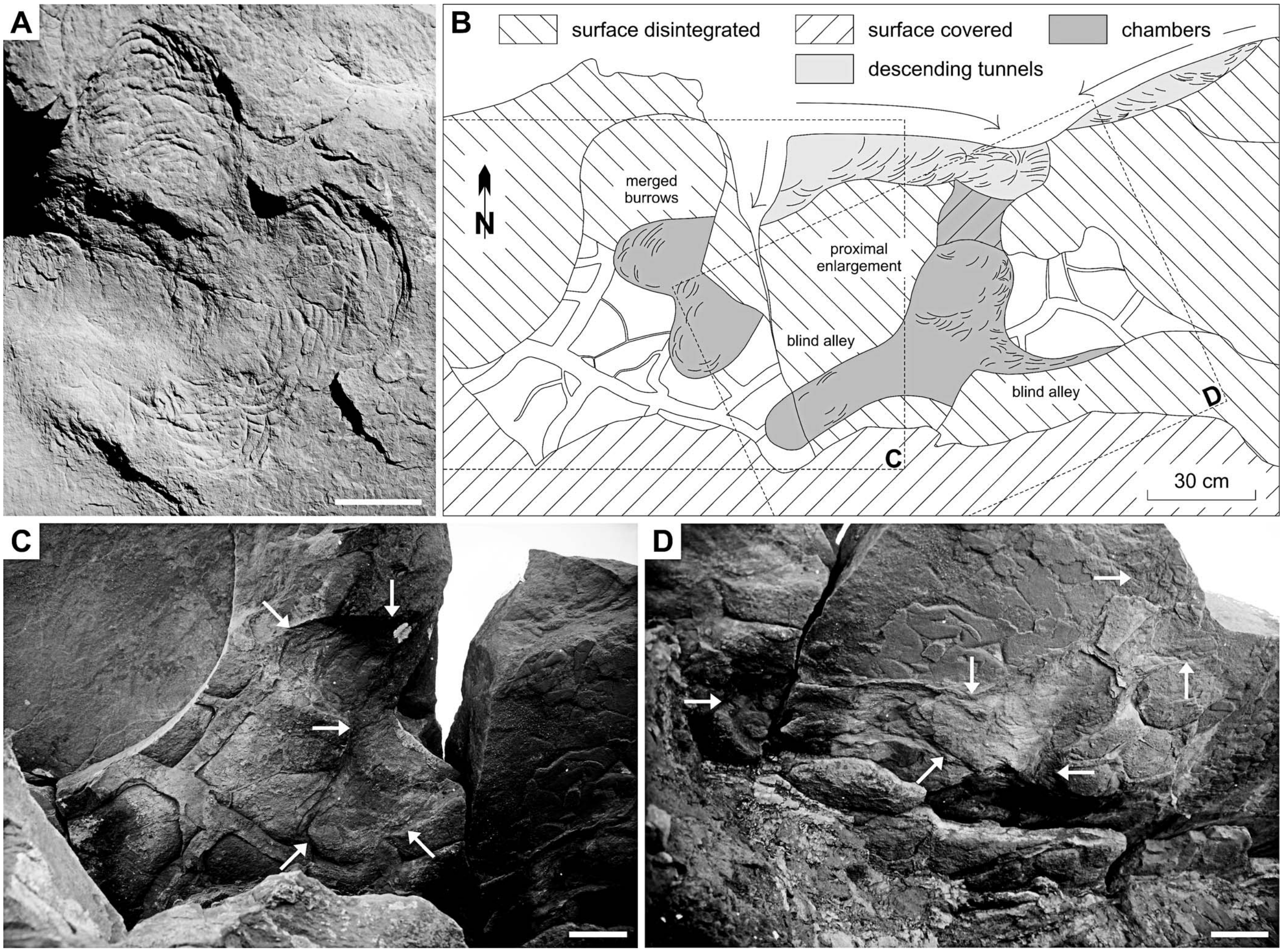


FIGURE 7—Terminal chamber architecture evidenced from scratch-mark patterns at the lower surface of sandstone bed 11b at CDUE locality 29, concave hyporeliefs. A) Burrow terminus with three alcoves in orthogonal arrangement. Note distal-most part of slightly inclined tunnel from the left. B–D) Complex chamber system including merged burrows, enlarged bypass area and blind tunnels interconnected by descending tunnels allowing entry from different directions. Photographs illustrate outcrop situation with arrows outlining scratched areas. A, C, and D, scale bar = 10 cm.

define the deepest parts of the burrow systems as actual terminal structures. Estimated from the most complete specimen (Fig. 7B) burrow termini covered areas of at least 1×1.5 m.

The maximum depth of the burrow system is difficult to assess. *In situ* burrows almost exclusively occur in bed 11b at CDUE locality 29 (Fig. 3A). The thickness of this bed ranges from 35 to 230 cm along the outcrop distance, and burrow sections are recorded in all levels, from the top to the base of the unit. Providing evidence that all burrows in this unit belong to the same generation of tetrapod activity is impossible because of the multistoried channelized sandstone, which includes erosional surfaces and intercalations of overbank fines. A minimum depth of the burrow systems of 51 cm is calculated using an averaged tunnel inclination (20°), the length of the most continuously exposed tunnel segment (115 cm), and a hypothetical height for the terminal chamber (12 cm, according to the maximum observed tunnel height). Assuming that sand within abandoned channels was the preferred medium for tunnel construction and intercalated overbank muddy sediment for construction of chambers (Figs. 5A, C; 7), this type of burrow should be restricted to $\geq$40-cm-thick sandstone beds. In this context, isolated short burrow segments in thin layers of sandstone (Fig. 3A) could be interpreted as tunnels that had been abandoned due to inappropriate media. The rarity of sites where the medium was ideal for the digging of burrows may be the reason why there are so many concentrated in a single area.

The Argana burrows are remarkable with respect to their sharp outlines and distinct scratch marks suggesting that their construction took place in a cohesive material. Thin sections of the host rock exhibit fine- to medium-grained quartz sandstones with $<$15% of intergranular carbonate cement. The aggregations are densely packed, moderately to well sorted, and composed of strikingly angular grains. As synsedimentary cementation cannot be determined, we propose that tightly interlocked angular grains, perhaps in conjunction with adhesive water, produced a cohesive and stable medium at the time of burrowing.

Burrow Function

Tetrapods adopt a temporary or permanent subterranean lifestyle mainly for reasons of thermoregulation, shelter from predators, reproduction (breeding and maturing juveniles), and feeding (searching and storing of food) (Voorhies, 1975; Reichman and Smith, 1990; Meadows, 1991; Riese et al., 2011). Burrows often meet multiple needs, which makes the distinction of the primary purpose of fossil examples difficult (Groenewald et al., 2001; Tałanda et al., 2011). The Argana burrows are no exception and allow very few inferences in this respect.

The complexity and precision of the burrows suggest their construction as long-term dwellings by accomplished burrowers. The smoothed floors indicate that the tunnels were frequently used

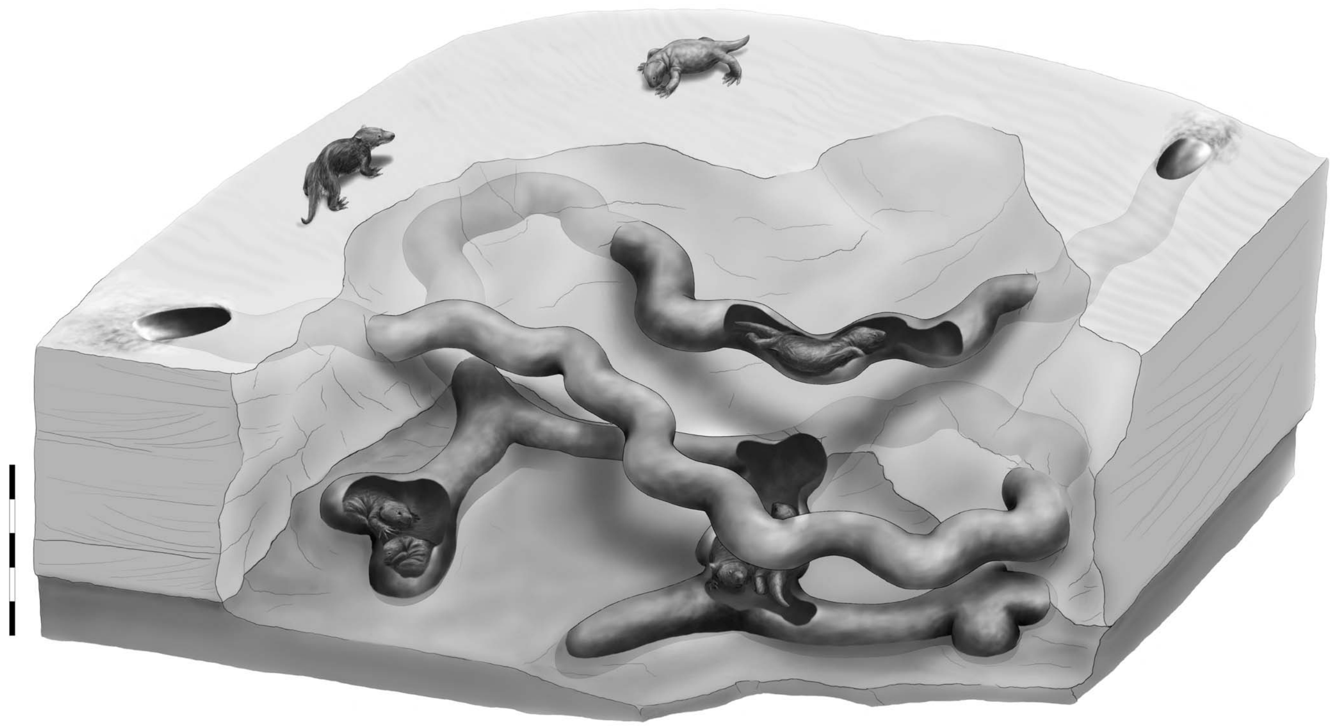


FIGURE 8—Reconstruction of the Middle Triassic tetrapod burrow system from the Argana Basin with cohabitant procolophonids or therapsids. Scale bar = 50 cm.

passageways to the surface. Such behavior is typical for aboveground foraging animals (DeBlase and Martin, 1981).

The large size of the burrow systems with separate and branched terminal chambers containing grouped alcoves and enlarged bypass areas suggests they were excavated by multiple individuals. Although communal behavior appears to be evident, the extent of cooperation between the occupants (reproduction, parental care, division of labor) is impossible to determine from the data. Similarly, there are a variety of possibilities regarding the function of the numerous dead-end excavations including resting, nesting, food storage, and defecation, but neither the shape nor the size clarifies the purpose of these structures.

The preferred position of terminal chambers in possible moisture-retaining overbank fine-grained sediment might be functionally interpreted in terms of having provided shelter from seasonally hot and dry climatic surface conditions, especially against the background of frequently bent tunnels (Meyer, 1999). We cannot exclude, however, the possibility that the burrow excavators preferred muddy sediment because it was more cohesive than the fine sand and could support large chamber structures without the threat of collapse. Dwelling structures excavated deep into sand does also not exclude that the tracemakers intended their use as a refuge from predators.

Tracemaker

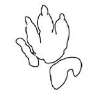
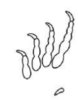
Body fossils have not yet been found with the Argana burrows. The only known tetrapod skeletal remains from the Aglegal Member (T4) of the Timezgadiouine Formation belong to an incomplete cyclotosaurid skull (Jalil, 1999; Jalil et al., 2009). These usually large temnospondyls are unlikely burrowers for anatomical and ecological reasons (Schoch and Milner, 2000). Consequently, evaluation of the potential trace-makers of the Argana burrows has to rely on evidence other than bones.

Given that burrow cost increases with the volume of excavated soil (Vleck, 1981), fossorial tetrapods often excavate tunnels in the diameter of their body size (Andersen, 1982; Laundre, 1989; White, 2005). This relationship is applied to the Argana burrows, especially since the dimension and arrangement of the scratch marks argue for tracemakers

TABLE 1—Characteristics of the Argana tetrapod burrows (checklist keys adapted from Miller et al., 2001).

Architecture	Simple entrances; partially spiral and superimposed high frequency sinusoidal tunnels; complex terminal chambers
Orientation	Subhorizontal to moderately inclined (≤30°)
Dimension	Tunnel: 11–20 cm in diameter; ≥115 cm in length
Width:height	1–2 (tunnel)
Cross section	Planoconvex to flattened biconvex (tunnel)
Terminal chamber	Yes; complex, multiply branched, with blind alleys and alcoves
Branching	Tunnel: Y-shaped; immediately above terminal chamber
Number of entrances	Probably 2, maybe more
Surface features	Groove-type scratch marks on sides and tops; more or less perpendicular to the direction of advance
Lining or mud chips	None
Density	Burrow systems, 2.5–4.5 m wide, 1–3 m laterally spaced
Amount of variation	Little
Animal in burrow	No
Environment	Alluvial plain, braided river
Age	Middle Triassic

TABLE 2—Tetrapod footprints from the Aglegal Member (T4) of the Timezgadiouine Formation defined by maximum pes length, generalized pes imprint morphology, and potential trackmakers (adapted from Klein et al., 2011).

Ichnotaxon	Potential trackmaker	Maximum pes length (T4)	Pes imprint morphology
Chirotherium barthii	Archosauria: Avemetatarsalia	22 cm	
Isochirotherium coureli	Archosauria: Crurotarsi	23 cm	
Synaptichnium isp.	Archosauriformes or Archosauria: Erythrosuchidae or Rauisuchia	9.5 cm	
Atreipus-Grallator	Dinosauromorpha	1.3 cm	
Rotodactylus isp.	Dinosauromorpha or Lepidosauromorpha	3.4 cm (digits II–IV)	
Rhynchosauroides isp.	Archosauromorpha or Lepidosauromorpha	3.0 cm	
Procolophonichnium isp.	Procolophonida or Therapsida	2.3 cm	

that corresponded in size to that of the tunnels, i.e., <20 cm wide and ~12 cm tall. The maximum trunk length (distance between shoulder girdle and acetabulum) can be estimated to 22.5 cm, which is half of the maximum wavelength of the tunnel sinuosity, considering that quadrupedal tetrapods with longer trunks would have had great difficulty moving through tunnels of this form. Correspondingly sized early amniotes are known to have left footprints ranging from 50 to 70 mm in length (Demathieu, 1970; Haubold, 1971; Demathieu and Oosterink, 1983; Avanzini and Renesto, 2002; Voigt, 2005; Voigt et al., 2007).

Tetrapod footprints from strata closely associated with the burrows from CDUE locality 29 are assigned to the ichnotaxa *Chirotherium*, *Isochirotherium*, *Synaptichnium*, *Atreipus-Grallator*, *Rotodactylus*, *Rhynchosauroides*, and *Procolophonichnium,* indicating Archosauriformes or Archosauria, Dinosauromorpha, Lepidosauromorpha, and Procolophonida or Therapsida (Klein et al., 2011; Table 2). Due to their large size, trackmakers of *Chirotherium*, *Isochirotherium*, and *Synaptichnium* can be excluded as potential producers of the Argana burrows. Dinosauromorph tetrapods with functionally tridactyl autopodes and extended middle digit as reflected by imprints of the *Atreipus-Grallator* morphotype are also rather unlikely burrowing animals (Sereno and Arcucci, 1994; Haubold and Klein, 2000; Gand and Demathieu, 2005). Trackmakers of *Rotodactylus* or *Rhynchosauroides* cannot be definitely ruled out as burrowers by the size or morphology of their footprints, however, to our knowledge, there is no report on fossorial behavior of Triassic Lepidosauromorpha or Dinosauromorpha. Such activity has been proposed only for some Cretaceous dinosaurs (Varrichio et al., 2007; Martin, 2009; Huh et al., 2010). The most likely candidates for producing the Argana burrows are the potential trackmakers of *Procolophonichnium* based on body size, length of manus and pes, digit proportions, and robust claws inferred for these animals from other Triassic footprint records (Demathieu and Oosterink, 1983). *Procolophonichnium* is usually referred to procolophonids (Haubold, 1971; Demathieu and Oosterink, 1983), though therapsids are potential producers as well considering the similarity between *Procolophonichnium* tracks from the Argana Basin (Klein et al., 2011) and probable therapsid footprints from the Middle-Late Triassic of Brazil (Silva et al., 2008).

Tetrapod burrows from Triassic strata are mainly attributed to non-mammalian therapsid tracemakers based on associated skeletal remains (Groenewald et al., 2001; Damiani et al., 2003) or overall resemblance to burrows whose therapsid origin is reliably known (Hasiotis et al., 2004; Colombi et al., 2008; Modesto and Botha-Brink, 2010). A few studies cite procolophonids as producers of Triassic burrows (Stanistreet and Turner, 1979; Groenewald, 1991; Sidor et al., 2008) or consider this as a possibility (Miller et al., 2001). Fossorial behavior is widely accepted for various non-mammalian therapsids (Kemp, 2005), whereas possible adaptations for a burrowing lifestyle in procolophonids, such as the pronounced overbite and robust inner digits of *Procolophon trigoniceps* Owen, 1876 from the Triassic of Antarctica and South Africa (Colbert and Kitching, 1975; deBraga, 2003), seem not to be adequately considered.

Apart from size and inclination of the tunnels, there are no commonalities of the Argana specimens with previously described Permo-Triassic therapsid burrows (Smith, 1987; Groenewald et al., 2001; Hasiotis et al., 2004; Tałanda et al., 2011). The bilobed floor of cynodont burrow casts (Groenewald et al., 2001; Damiani et al., 2003) significantly differs from the flat-floored tunnels of the Argana burrows. Neither Y-shaped tunnel junctions nor branched terminal chambers with transverse scratch marks have ever been reported from non-mammalian therapsid burrows. A final decision on the producer of the discussed burrows is currently impossible, but procolophonids are at least as good candidates as therapsids.

Paleoenvironmental Interpretation of Burrow Sites

During the mid–Triassic, Northwest Africa was situated in the northern tropical zone governed by a strongly seasonal climate due to the Pangean megamonsoon (Parrish, 1993; Golonka and Ford, 2000; Preto et al., 2010). The red beds of the Aglegal Member (T4) of the Timezgadiouine Formation indicate deposition under predominantly semiarid climatic conditions with alternating dry and wet periods (Hofmann et al., 2000). This is supported by the sedimentological analysis of the burrow-bearing Taghrot Bizgarene hill section. Under these circumstances, seasonal aridity with extreme diurnal temperature fluctuations has to be considered as a major impetus for small tetrapods to shelter in the ground. The burrows give evidence for significantly varying water tables and markedly ephemeral deposition in central parts of an active sedimentary basin. There is potential for the reconstruction of ancient hydrological and climatic conditions in the study area through a more detailed analysis of the spatial and temporal distribution of these burrows, especially in view of the fact that isolated segments of similar tetrapod burrows have already been observed in the Upper Permian Ikakern Formation (S. Voigt, personal observation, 2010) as well as in the Tadrart Ouadou Member (T6) of the Upper Triassic Bigoudine Formation (Olsen and Et Touhami, 2008).

CONCLUSIONS

Complex tetrapod burrow systems have been discovered in Middle Triassic red beds of the Timezgadiouine Formation in the Argana Basin of central Morocco. Enlarged terminal chambers with multiple branches and grouped alcoves indicate their construction and use as subsurface dwellings by gregarious animals. As such, the findings represent the second oldest record of communal fossorial behavior in tetrapods and the oldest example from low-latitude areas. The main conclusions drawn from this study are: (1) The described burrows are unique by their lateral sinuous tunnels descending to complex terminal chambers with clusters of alcoves and distinct transverse scratch marks; (2) sturdy, small-bodied ($<$25 cm gleno-acetabular distance), procolophonids or non-mammalian therapsids are the most likely tracemakers; (3) complexity and precision of the excavations classify the constructors as accomplished burrowers; (4) thick interbedded sand and mud along the margins of ephemeral streams were the preferred media and site for the construction of this type of burrow; and (5) in equatorial regions of Pangea, fossorial behavior as refuge from predators or shelter from climatic extremes developed in terrestrial tetrapods not later than the Mid-Triassic.

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