

Hettangian tetrapod burrows from the continental Steierdorf Formation at Anina, western Romania

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Very large, sparsely distributed, sinuous, gently dipping and occasionally branching tunnels with subordinate swells, as well as possible chambers and scratches, are described from the Hettangian Dealul Budinic Member of the Lower Jurassic continental Steierdorf Formation at Anina in the South Carpathians, Romania, and are interpreted as tetrapod burrows. No bone remains have been found in association with these structures. The morphology and large dimensions of the burrows suggest that the trace-makers were sauropsid amniotes, most probably either crocodyliforms or small-sized basal neornithischian dinosaurs, although their therapsid affinities, despite being less likely, cannot be discarded either. The age, large size and probable origin of these burrows add important information to a poorly documented period of the evolution of tetrapod fossoriality. It may be suggested that within a relatively short time interval following the Triassic-Jurassic extinction event, when environmental conditions were still marked by strongly seasonal climate with prolonged droughts as well as extreme moisture and temperature fluctuations, fossorial habit probably became yet again an endurance strategy for burrow makers.

Key words: Tetrapod burrows, therapsids, crocodyliforms, dinosaurs, Lower Hettangian, Steierdorf Formation.

INTRODUCTION

Tetrapods produce burrows for variety of reasons that include escaping environmental fluctuations and harsh conditions, finding food, evading predators, or rearing of young (e.g., Voorhies, 1975; Hildebrand, 1985; Miller et al., 2001; Varricchio et al., 2007). Reports of large penetrative tetrapod burrows in ancient continental deposits are relatively rare, however, especially compared with the extensive literature on tetrapod trackways produced primarily in the same environments. Burrows attributed to the activity of therapsids are the most commonly reported such structures (e.g., Voorhies, 1975; Smith, 1987; Groenewald, 1991; Groenewald et al., 2001; Hasiotis et al., 2004; Tanner and Lucas, 2009; Bordy et al., 2011; Tałanda et al., 2011; Voigt et al., 2011). In comparison, the fossil record of reptile burrowing remains relatively sparse (Hasiotis et al., 2004), and only a few amphibians (mainly from the Permian) are known to have produced burrows preserved in the fossil record (e.g., Olson, 1971). Recently, a spectacular find of Mid-Cretaceous trace and body fossil evidence of burrowing in

a dinosaur expanded the known range of non-avian dinosaur behaviour to fossoriality (Varricchio et al., 2007; Fearon and Varricchio, 2015).

As yet, Lower Jurassic strata yielded only few evidences of fossorial behaviour in tetrapods, and these came exclusively from red beds formed in an arid climate (Lucas et al., 2006; Tanner and Lucas, 2009). The Lower Jurassic continental beds of the Reia Basin at Anina, Romania, grouped in the Steierdorf Formation (Figs. 1–3) represent, however, a case of deposits accumulated under a moister climate than those yielding the Early Jurassic tetrapod burrows from North America, as the Anina succession records a switching from semi-arid to seasonal/monsoonal and finally to more humid conditions up-section. Vertebrate body fossils have yet not been found in these deposits, most probably because of unfavourable preservational potential. Fortunately, the preservation of different trace fossils within these continental deposits allows a more complete understanding of the local palaeoecosystem. These trace fossils include invertebrate traces and tetrapod tracks (Popa, 2000c; Pie kowski et al., 2009). Popa and K dzior (2006) briefly reported possible vertebrate burrows occurring in the Steierdorf Formation, distinguishing two morphotypes of burrows: linear and spiral ones. However, the so-called “spiral burrows” appear to represent a mere diagenetic phenomenon, associated with oxidation of sideritic nodules. More detailed description and interpretation of these burrows is the aim of current paper.

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Fig. 1. Localization of Reșița Basin and of Anina in the Southern Carpathians, Romania

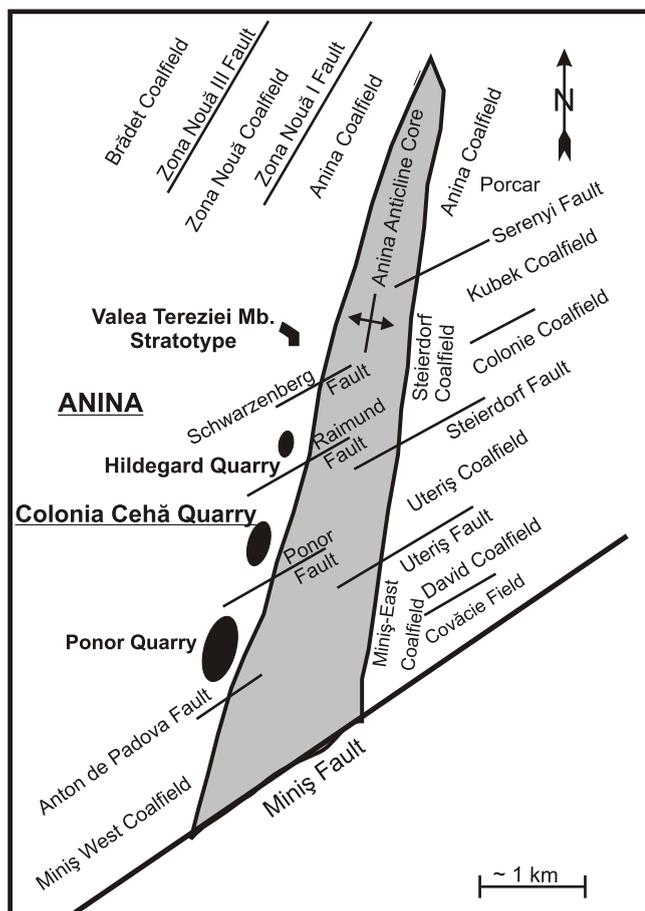


Fig. 2. The local geological structure at Anina, emphasizing the Anina anticline with Permian core and locally developed Steierdorf Formation coalfields separated by faults, with the Colonia Ceh Quarry marked (simplified from Popa, 2009)

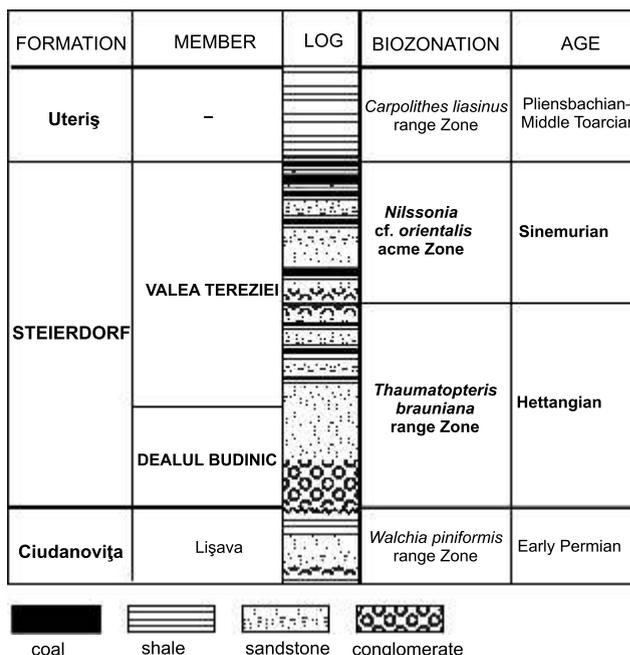


Fig. 3. Synthetic lithostratigraphic log of the Steierdorf Formation

GEOLOGICAL SETTING

The burrows described herein were discovered in the Colonia Ceh Quarry, an open cast mine in Anina, Cara -Severin County (Fig. 2). The open cast mine, dug in N–S direction along the western flank of the Anina Anticline, revealed a spectacular section of the Steierdorf Formation (Hettangian–Sinemurian) with both of its subunits, the lower Dealul Budinic and the upper Valea Tereziei members. The Colonia Ceh Quarry lays between two major faults, transversal to the Anina Anticline, the Ponor Fault to the south and the Raimund Fault, northwards. Additionally, in the Colonia Ceh Quarry, both the flank of the Anina Anticline and the deposits of the Steierdorf Formation are cut by numerous transverse, parallel, normal and reverse faults into a series of small tectonic blocks (Figs. 2 and 5C). The beds crop out almost vertically.

The Lower Jurassic (Hettangian–Sinemurian) Steierdorf Formation is a purely continental succession of siliciclastic, in its upper part also coal-bearing, sediments, formed in an intra-mountain depression. This unit forms part of the sedimentary infilling of the Re i a Basin, also known as the Re i a–Moldova Nou sedimentary zone, the most important sedimentary basin of the Getic Nappe (S ndulescu, 1984; Bucur, 1991, 1997; Popa and K dzior, 2008; Figs. 1–3). The Steierdorf Formation unconformably overlays the Lower Permian Ciudanovi a Formation and it is conformably overlain by the Pliensbachian–Middle Toarcian Uteriș Formation (Bucur, 1991, 1997; Popa and K dzior, 2008; Fig. 3), a unit that includes black, bituminous shales with sideritic intercalations, which were the target of open cast mining.

The Steierdorf Formation is divided into two members, the Dealul Budinic Member (?Rhaetian–Hettangian in age), and the Valea Tereziei Member (Hettangian–Sinemurian in age; Fig. 3; Popa, 2000a, b; Popa and van Konijnenburg-van Cittert, 2006). Age of the fossil-barren Dealul Budinic Member is inferred from its stratigraphic position and conformable setting below the overlying fossiliferous Valea Tereziei Member. The Dealul Budinic Member is dominated by red and grey-yellowish-olive conglomerates, microconglomerates and sandstones with red mudstone intercalations; the coarser beds originated in alluvial fans and low-sinuosity river channels, whereas the fine-grained deposits accumulated at the coalescence of the alluvial lobes or in topographic lows on top of the coarser-grained alluvia (Figs. 3 and 4; K dzior and Popa, 2013). The uppermost part of Dealul Budinic Member is marked by a pyroclastic/tuffitic layer, material of which the infilling of the burrows reported in this contribution is largely made of.

The overlying Valea Tereziei Member represents the proper coal measure which was heavily mined at Anina for bituminous coals since 1792, and is composed of grey sandstones, clays, coals, conglomerates and microconglomerates (Fig. 3),

formed in fluvial and lacustrine environments. The fossil record of the Valea Tereziei Member includes a rich bryophyte, pteridophyte and gymnosperm compressive flora, especially in Anina (e.g., Popa, 2000a, b; Popa and van Konijnenburg-van Cittert, 2006), as well as traces of insect-plant interactions (Popa, 2009; Popa and Zaharia, 2011). From a phytostigraphic point of view, the Hettangian age of the lower Steierdorf Formation is indicated by the *Thaumatopteris brauniana* assemblage, while the Acme Zone with *Nilssonia cf. orientalis* identified in its upper part points to the Sinemurian (Fig. 3).

The Dealul Budinic Member, in which the burrows are dug in, is dominated by massive, matrix-supported conglomerates, very coarse- to coarse-grained structureless sandstones and laminated siltstones and mudstones (Fig. 4), and is regarded as representing largely an alluvial fan environment (K dzior and Popa, 2013). Depositional processes were dominated by high energy viscous flows operating in the proximal parts of the alluvial fan, active braided channel flows developed at middle to distal reaches, transitional flows between fluvial and debris flow processes, and sheet flows occurring during flooding periods (K dzior and Popa, 2013). The presence of the fine-grained clastics (mudstones and siltstones) might be related to the occurrence of local depressions with intermittent water bodies and other common areas of fine-grained sedimentation, usually situated at coalescence zones of individual lobes (Neves et al., 2005) or within depressions created on the top of the alluvial fans (Rachocki, 1981). The deposition of the mud might have also occurred after heavy rainfalls, thus could be directly related to mud flows (Rachocki, 1981). Common desiccation cracks point to recurrent water-table fluctuations.

Massive or laminated red/violet mudstones (ca. 180 cm thick) occur in the upper part of the Dealul Budinic red bed complex. These represent the host sediment of the burrows (Figs. 4 and 5A, C–E). The red colouring of the sediments is indicative of oxidizing conditions, connected with deposition of detritic hematite under a warm climate with seasonally distributed rainfalls (van Houten, 1961), and can be linked to monsoonal conditions as was postulated by Mateescu (1958) and Pie kowski et al. (2009). Indeed, this area was located between 20 and 30° northern latitude during the Early Jurassic (Popa and van Konijnenburg-van Cittert, 2006). The lack of well-preserved plant remains and lack of pedogenic horizons within the Dealul Budinic Member points to a high oxidation level combined with rapid deposition and unstable substrate. Additionally, periodic and heavy rainfalls leading to erosion might have contributed to the washing out (removal) of both the incipient soils and of the plants remains not yet stabilized by well-developed root systems.

Above the reddish mudstone beds, there is a 60–120 cm thick grey mudstone layer containing pyroclastic material. The grey mudstone is usually massive, and sporadically presents very faint flat lamination and ripple-drift cross-lamination. X-ray analysis shows that it is largely composed of kaolinite (96%) with quartz and feldspar grains. This layer does not correspond to a direct effusive deposit, but instead represents a rede-

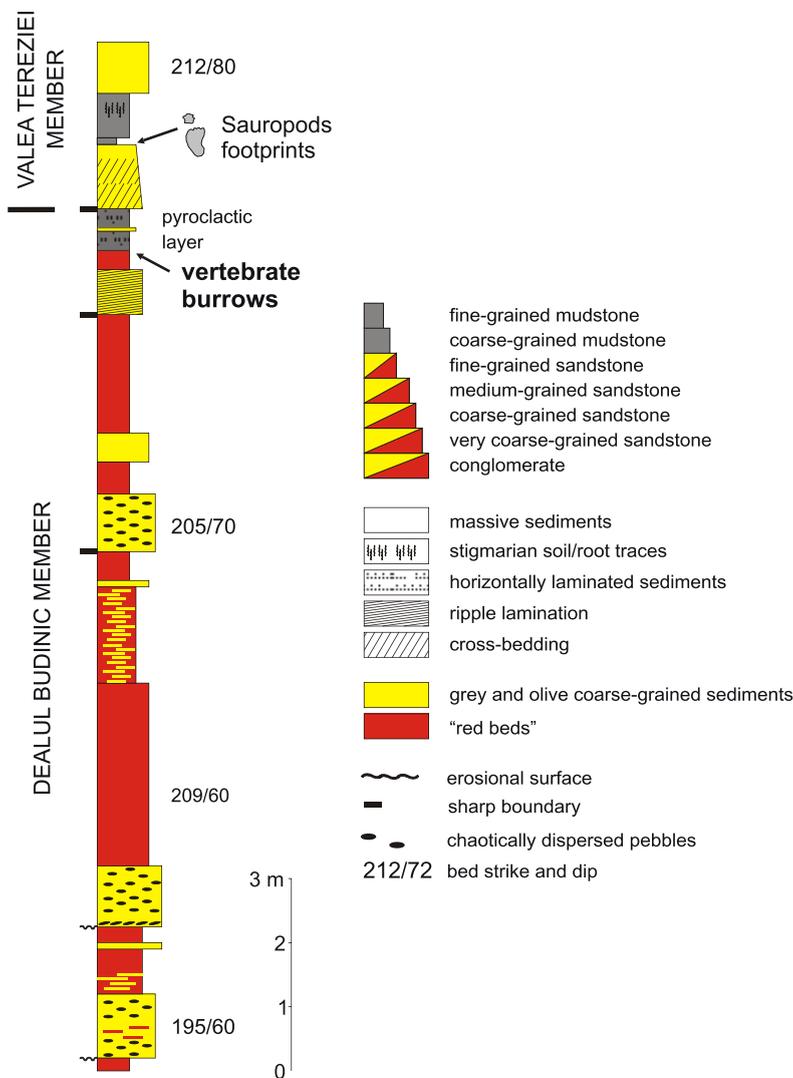


Fig. 4. Local stratigraphic log of the Dealul Budinic Member of the Steierdorf Formation, with position of the vertebrate burrows in Colonia Ceh Quarry highlighted

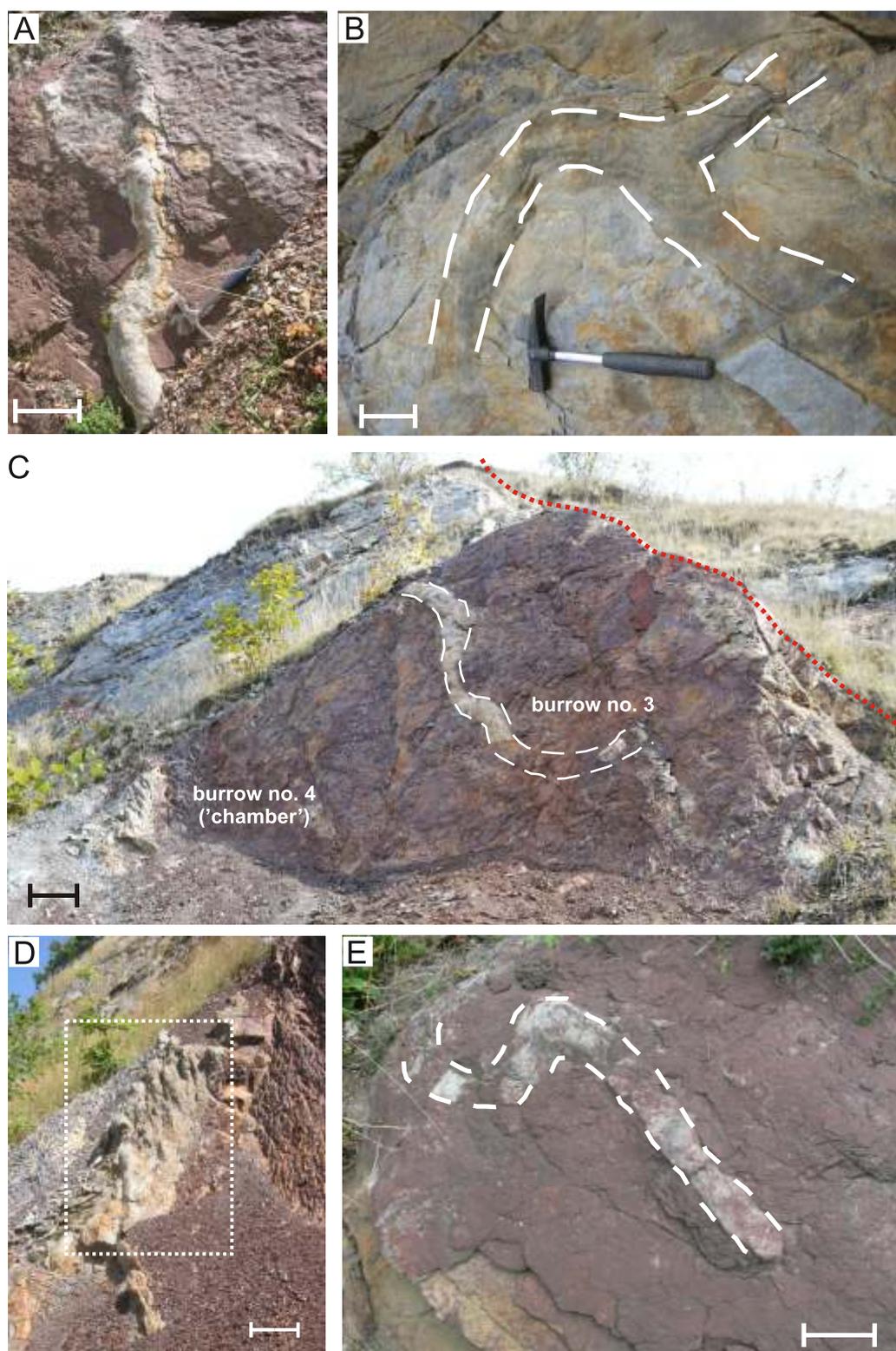


Fig. 5. Aspects of the amniote burrows from the Lower Jurassic Steierdorf Formation, Anina

A – burrow no. 1, simple sinuous tunnel with occasional swells, with another tunnel running underneath and only partly exposed; northern corner of the Colonia Ceh Quarry, eastern flank, Anina (length of hammer, used for scale: 290 mm); **B** – winding, dichotomously branched burrow no. 2; northern tip of the Colonia Ceh Quarry, eastern flank, Anina (length of hammer: 270 mm); **C** – burrow no. 3 (winding) and burrow no. 4 (possible “chamber”; for details, see Figs. 5D and 6); middle part of the Colonia Ceh Quarry, eastern flank, Anina; the red dotted line represents a local fault, separating two small, local tectonic blocks; the site occurs in the proximity of the sauropod tracks described by Piekarski et al. (2009) from a slightly higher horizon; **D** – burrow no. 4 (possible “chamber”-like structure); middle part of the Colonia Ceh Quarry, eastern flank, Anina; boxed area marks the position of close-up details shown in Figure 6A–C; **E** – burrow no. 5, winding form, showing swells at the turns; Colonia Ceh Quarry, eastern flank, Anina; scale bar represents 10 cm (B), 20 cm (A, D, E) and 40 cm (C), respectively

posited material, as proven by the occurrence of sedimentary structures indicative of deposition from current (Fig. 4). These tuff-bearing sediments were deposited in an intermittent shallow lake and they provided part of the infilling material of the burrows.

The occurrence of grey mudstones with volcanic tuffs in the top of the Dealul Budinic Member heralds a major change in depositional systems and palaeoclimate. From that level upwards, the climate changes to a more humid one as suggested by the coal-bearing character of the overlying Valea Tereziei Member.

DESCRIPTION OF THE BURROWS

In total, five structures identified as potential burrows, numbered in this paper from 1 to 5 (Fig. 5; see below), were identified exposed within different tectonic blocks along the eastern flank of the Colonia Ceh Quarry:

- burrow no. 1 is the northernmost occurrence, showing subordinate swells (Fig. 5A); a second faintly visible burrow runs underneath burrow 1 and is only partly exposed. It is followed towards the south, sequentially, by
- burrow no. 2, a dichotomously divided burrow with possible scratch-marks (Fig. 5B); then by
- burrow no. 3 which represents the longest burrow structure observed in the field (Fig. 5C); and finally by
- structure no. 4, a tentatively identified, possible burrow represented by a large, irregular chamber-like structure (Figs. 5C, D and 6; see below). Burrows 3 and 4 occur in the same outcrop where sauropod footprints have also been recorded recently by Pie kowski et al. (2009). On its turn,
- burrow no. 5, with weak swells, is located again in the northern end of the Colonia Ceh Quarry, close to burrow no. 1 (Fig. 5E).

Most of these structures are simple, linear to slightly sinuous, very large or giant tunnels (according to the terminology of Miller et al., 2001), ellipsoidal to circular in cross-section; occasionally, the cross-section is slightly asymmetrical, with a somewhat flattened surface (“floor”) facing downwards and a rounded “roof”. They are up to 7 m long, and usually 10–15 cm wide, reaching in places about 20 cm (Fig. 5C). These burrows are not cross-cutting and lack evidence for any coiling or spiralling. Occasionally, however, the burrows can be dichotomously branching. In places the burrow diameter increases and swells can be observed (Fig. 5A, E). The burrows largely follow the bedding plane; in cases they are inclined relative to the bedding, the inclination angle remains very small. In most instances the burrows occur along one bedding plane, but locally these can be distributed superposed at two separate levels (Fig. 5A). The tunnels are usually built by longer and straighter segments linked by shorter, obliquely oriented connecting parts. While the length of the individual straight segments varies between 40 and over 60 cm, the oblique sections, representing the turning parts of their trajectories, are less than 30 cm long; these sections join the longer segments at angles ranging from about 38 to 55°. In places, knobby lining can be observed (Fig. 5A, E); this can be attributed either to diagenetic shrinkage or to the activity of commensal organisms (likely, invertebrates). All burrows are filled with a massive, structureless, noncalcareous grey mudstone with quartzose sandy admixture. Burrow fill (grey pyroclastic sandy mudstone) is lithologically very distinct from the host rock (a red-violet mudstone) and is reminiscent of the overlying mixed pyro-siliciclastic deposits.

Besides the more common, linear, sinuous forms, a large (40 cm in diameter), isolated irregular structure was also found (Fig. 5D). It differs from the common tunnel-like structures described before in that it appears to be both shorter and wider, suggesting a more “chamber”-like architecture; it shares, however, with the tunnels their similar, chromatically and lithologically distinctive nature of the infilling sediments (see above). Its spatial relationship to the linear burrows unfortunately re-

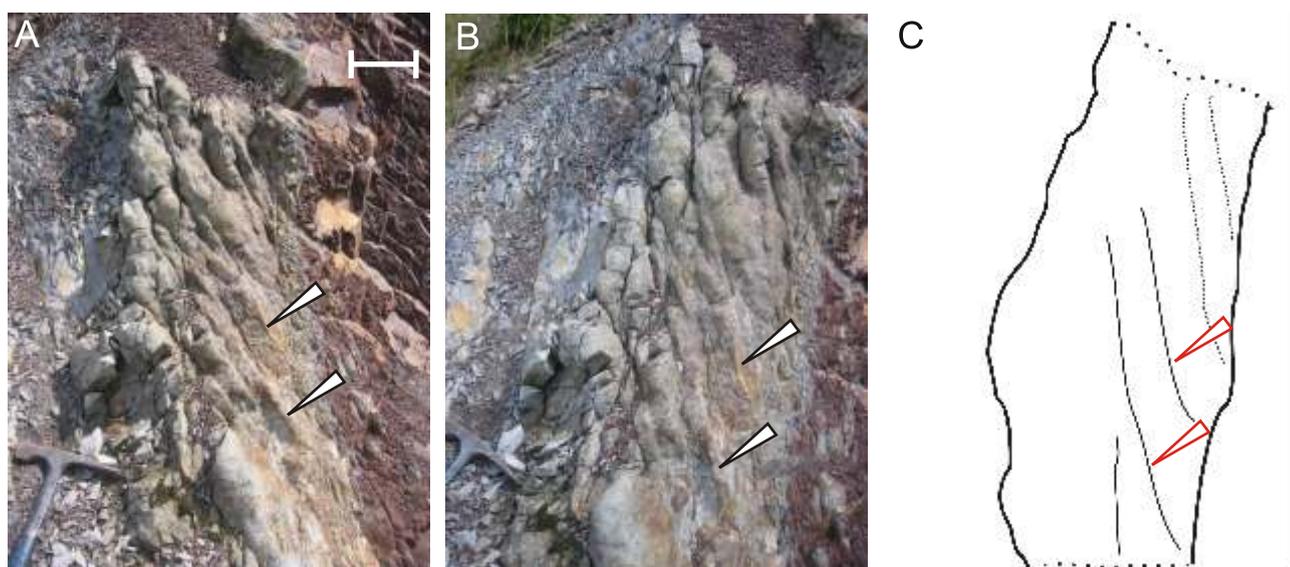


Fig. 6. Details of the “chamber”-like structure (burrow 4) from the Lower Jurassic Steierdorf Formation, Anina

A, B – close-up images of structure 4 (possible “chamber”; Fig. 5C, D), showing compactional deformations and ridge-like longitudinal traces interpreted as possible digging traces (arrowed); C – interpretative line drawing of the surface of structure 4 (possible “chamber”), with the most prominent oblique ridges (interpreted as potential digging traces; solid line) arrowed; dotted lines mark further possible oblique digging traces; scale bar represents 10 cm

mains uncertain, as it occurs isolated from, and without obvious connections to, any of the curvilinear tunnels. The “chamber” shows irregular protuberances, and in places also presents sharp, roughly parallel longitudinal ridges (Fig. 6) which may potentially represent scratch marks. These ridges are oriented obliquely to the main axis of the structure, and widely spaced (Fig. 6). The morphology of the crests, together with their dimension relative to the diameter of the structure, suggest that they probably represent marks of the digging paws themselves instead that of the individual digits/claws. It must be emphasized, nonetheless, that identification of this structure should be considered very tentative for the moment, pending future discovery of similar, possibly better preserved traces.

As preserved and observed in the field, the distribution of the linear burrows is rather patchy; however, the tectonized nature of the outcrops with number of faults should be also taken to consideration in that respect (Fig. 5A). Nevertheless, based on our observations concerning the largest accessible continuous outcropping surface with burrows, it is clear that these structures are widely spaced, and do not form more complex and crowded systems as do some of those described from the Triassic–Jurassic in other parts of the world (e.g., Groenewald et al., 2001; Hasiotis et al., 2004; Tanner and Lucas, 2009).

INTERPRETATION AND DISCUSSIONS

To begin with, we have considered alternative, non-biological “zero hypotheses” for the origin of these structures, such as syndepositional or erosional origin, or else diagenetic origin (i.e., concretions).

These alternative hypotheses can be rejected because it is hard to conceive how sedimentary or erosional (scour-and-fill) processes could have produced such relatively regular tunnel-like shapes, closed from all sides, and filled with sediment that is completely different from the surrounding matrix. Post-depositional compaction processes can produce indeed load casts (i.e., ball structures), but they would not be that long, regular and continuous in development as documented by the structures observed at Colonia Ceh Quarry (although it is certainly possible that compaction and post-depositional deformation could have influenced, secondarily, the shape of the structures described above). Finally, structures originating through differential post-depositional chemical cementing of the sediments (i.e., concretions) are characterized usually by the occurrence of the same basic petrographic type within the concretions and the surrounding matrix, which is definitively not the case of the structures described in this contribution. To conclude, a non-biogenic (primary sedimentary, erosional, or diagenetic) origin for the Dealul Budinic Member tunnel-like structures can be reliably discarded, and these are thus considered in the following discussions as structures of biogenic origin (i.e., burrows).

After establishing the biotic origin of these structures, different origins of the burrows were taken into consideration. Due to the purely terrestrial setting and the age of the deposits that host the structures, the list of potential trace makers is rather short, and it includes invertebrates – mainly arthropods such as crayfish, annelids and mollusks, as well as vertebrates – fishes, amphibians and amniotes (e.g., Hasiotis, 2003; Hembree, 2010). Most invertebrates can be excluded as trace-makers by the large size of the burrows and the absence of active, meniscate backfilling. Moreover, crayfish burrows (e.g., Hasiotis and Mitchell, 1993; Bedatou et al., 2008; Martin et al., 2008) consist of simple to complex architectures with varying degrees of

branch, chamber, and chimney (vertical entrance) development, combined with a variety of surficial morphologies, including knobby surfaces, scratch and scrape traces, mud- and lag-liners, pleopod striae, and body impressions, which is not the case in the Colonia Ceh burrows. Among fishes, lungfish burrow deeply to avoid desiccation during dry periods, producing vertical burrows about 10 cm in diameter (Romer and Olson, 1954) and with enlarged basal chambers (Johnels and Svensson, 1954), a morphology strikingly different from those described herein. Furthermore, fossil examples of lungfish burrows are commonly reported to be tied to lacustrine to regressive marginal marine depositional environments (e.g., Surlyk et al., 2008; Gaillard et al., 2013), unlike the sedimentary setting reported here for the Anina burrows.

On the other hand, tetrapod burrows are characterized by dominantly horizontal or subhorizontal branches (tunnels, *sensu* Hasiotis et al., 2004), gently sloping ramps and/or spiralled branches, with a near-circular cross-section. Usually, these burrows are dug into palaeosol levels, although they can also occur in other depositional environments such as ephemeral ponds (Hembree et al., 2005), abandoned braided fluvial channels (Martin, 2009), channel margins and overbanks (Hasiotis et al., 2004; Colombi et al., 2012), or sand dunes (Loope, 2006, 2008; Lucas et al., 2006). In all their characteristics, the Early Jurassic burrows from Anina correspond to the tetrapod burrow type and depart sharply from those of the crayfishes or lungfishes, leaving one or another group of tetrapods as potential trace-makers.

Among tetrapods, amphibians usually dig into the substratum to avoid body dehydration through evaporative water loss during drought periods, and such behaviour – supported both by ichnology and by skeletal adaptations – is already reported from the fossil record (see reviews by Gardner, 1999; Hembree, 2010; Maddin et al., 2013; Roček et al., 2014; Henrici, 2016; Chen et al., 2016). According to Hembree (2010), there is a remarkable parallelism between amphibian burrows and those of the lungfishes, both types being represented by subvertical shafts excavated into ephemeral pond deposits (see also Hembree et al., 2005); moreover, their sizes are relatively small (usually not surpassing 10 cm in diameter). In all these features, amphibian burrows differ from those reported herein from Colonia Ceh Quarry, and thus amphibians can be also excluded from the list of potential trace makers, leaving only members of the two major groups of amniotes as potential candidates for these: the sauropsids and the therapsids.

During Cenozoic times, the most important burrowing tetrapod group is that of the mammals. Meanwhile, during pre-Cenozoic times the widespread examples of burrowing mammals and their immediate therapsid ancestors (e.g., Voorhies, 1975; Smith, 1987; Groenewald, 1991; Groenewald et al., 2001; Miller et al., 2001; Damiani et al., 2003; Hasiotis, 2003; Hasiotis et al., 2004; Colombi et al., 2008, 2012; Tanner and Lucas, 2009; Sidor et al., 2008; Modesto and Botha-Brink, 2010; Hembree, 2010; Bordy et al., 2011; Tałanda et al., 2011; Liu and Li, 2013 and references cited therein) were seconded by different groups of “reptiles” (i.e., sauropsid amniotes) such as lepidosaurs (e.g., Lee, 1998; Kearney and Stuart, 2004; Martill et al., 2015; Yi and Norell, 2015), procolophonid turtle ancestors and turtles (e.g., Groenewald, 1991; de Braga, 2003; Sidor et al., 2008), or crocodyliforms (e.g., Gomani, 1997; Loope, 2008) as likely candidates for a burrowing habit. More recently, even dinosaurs were added to the list of burrowing Mesozoic tetrapods (Varricchio et al., 2007; Martin, 2009; Woodruff and Varricchio, 2011).

Except for the procolophonids and the snakes, all the other Mesozoic amniote groups listed above and known to exhibit

fossorial behaviour were present in the Early Jurassic (see Benton, 1993), and thus represent possible candidates for the trace maker of the Dealul Budinic Member burrows. Further narrowing down this list of potential candidates is possible taking into account the ethology of the burrowers (as manifested in the morphology of the burrows).

Burrowing habits evolved relatively early in the therapsid evolutionary line leading to mammals, and was probably one of the main factors allowing differential survival during the end-Permian events (e.g., Smith and Botha, 2005). Adaptations for digging and burrowing were identified, based on functional morphology, in several different pre-Cenozoic therapsid taxa. Such skeletal adaptations were reported in this clade from the Permian (the dicynodont *Diictodon*; Ray and Chinsamy, 2003) to the Late Jurassic (the theriomorph *Fruitafossor*; Luo and Wible, 2005) and the Late Cretaceous (indeterminate djadochtherian multituberculates; Kielan-Jaworowska, 1989); indeed, burrowing appears to be an ancestral behavioural trait at the level of cynodonts, if not that of more basal therapsids (Damiani et al., 2003).

Synapsid (including mammaliaform) burrows are among the best known pre-Cenozoic tetrapod subterranean dwelling traces. These were reported from deposits of the Upper Permian (Smith, 1987), the Permian/Triassic boundary (Damiani et al., 2003), and the Lower–Middle Triassic (e.g., Groenewald, 1991; Groenewald et al., 2001; Modesto and Botha-Brink, 2010; Fernandez et al., 2013) of South Africa, as well as from the Middle–Upper Permian of China (Liu and Li, 2013), the Lower Triassic of Antarctica (Miller et al., 2001; Hasiotis et al., 2004), the Middle Triassic of northern Africa (Voigt et al., 2011), the Middle and Upper Triassic of South America (e.g., Colombi et al., 2012; Krapovickas et al., 2013), the Upper Triassic of Europe (Tafanda et al., 2011), and the Upper Triassic (Hasiotis et al., 2004; Colombi et al., 2008), Lower Jurassic (Lucas et al., 2006; Tanner and Lucas, 2009) and Upper Jurassic (Hasiotis et al., 2004) of North America. The common characters of these traces are represented by the relatively complex geometry of the burrows, ranging from spirally descending tubular tunnels ending in an enlarged terminal chamber to networks of interconnected tunnels, shafts, oblique ramps and chambers; their cross-section is circular to ellipsoidal, frequently with a median threshold on the floor of the burrow, giving it an inverted U-shape; and the relatively small size of the cross-section, with its maximum diameter not surpassing 20–25 cm, and often averaging only 10–15 cm.

From the survey of the published pre-Cenozoic therapsid burrowing record it appears that there was a certain progression during time in characters such as degree of interconnections and types of branching represented in the burrows, characters that appear to develop complexity over time. The oldest burrows are relatively simple in geometry, represented by helically downward spiralling, but otherwise simple, unbranched tunnels from the Upper Permian, referred to the dicynodont *Diictodon* in South Africa (Smith, 1987) or to indeterminate, larger-sized dicynodonts in China (Liu and Li, 2013), and are followed by shallowly dipping, curvilinear tunnels from the Lower Triassic, referred to either the dicynodont *Lystrosaurus* (Groenewald, 1991; Bordy et al., 2011) or to indeterminate therapsids (Miller et al., 2001; Hasiotis et al., 2004; Sidor et al., 2008). Starting from the Early–Middle Triassic, therapsid burrow complexity increases; more intricate networks of interconnected tunnels and shafts are described from the Lower Triassic, referred to the cynodont *Trirachodon* (Groenewald et al., 2001), the Middle Triassic (therapsids or procolophonids; Voigt et al., 2011), the Upper Triassic (indeterminate therapsids; Hasiotis et al., 2004, or cynodonts; Colombi et al., 2012), and

the Lower Jurassic (indeterminate tritylodontid cynodonts; Lucas et al., 2006; Tanner and Lucas, 2009). This trend finally culminates with simple to complex networks of tunnels, shafts, ramps and chambers, described from the Upper Jurassic and attributed to indeterminate fossorial mammals (Hasiotis et al., 2004).

This time-correlated progression in burrow complexity appears to mirror evolutionary changes associated with the origin of the Mammalia (e.g., Kemp, 2005), and most probably reflects increase in complexity of social interactions, increase that occurred in the line leading to mammals, from asociality-subsociality in the Permian dicynodont *Diictodon* (Ray and Chinsamy, 2003), to aggregation and shelter sharing in the Early Triassic (Abdala et al., 2006; Viglietti et al., 2013), and finally to advanced gregarious behaviour in the Middle Triassic–Jurassic (Hasiotis et al., 2004; Voigt et al., 2011; Krapovickas et al., 2013). Moreover, it seems that digging complex burrow networks of advanced architecture, foreshadowing those of Neogene and Recent mammals, became a common behaviour among synapsids as early as the middle of the Triassic.

In light of these observations, the hypothesis of synapsid trace makers responsible for the Colonia Ceh Quarry burrows appears weakly supported at best; the Early Jurassic age of the burrows stands in contrast to their simple morphology, which is more reminiscent of those described from the Lower Triassic of South Africa than of those more complex ones from the Middle–Upper Triassic, let alone from the Jurassic. However, the dicynodonts, makers of the simpler burrow morphologies of the Permian–Early Triassic, dwindled dramatically after the Middle Triassic (e.g., Kemp, 2005; Ruta et al., 2013), and were largely extinct by the end of that period, being replaced by the more advanced tritylodontids and tritheledontids besides the derived mammaliaforms (Ruta et al., 2013). Although the youngest possible member of the dicynodonts was reported from the Lower Cretaceous of Australia (Thulborn and Turner, 2003), the occurrence of basal eucynodontians, similar to those responsible for South African Early Triassic burrows, in the Lower Jurassic of Europe is considered highly improbable, although not entirely impossible, and remains yet to be supported by the fossil record.

Furthermore, the Colonia Ceh Quarry burrows are larger (especially in length, and also slightly in cross-sectional diameter) than burrows customarily referred to derived mammal-like reptiles (cynodonts) and/or early mammaliaforms, and are also significantly larger than the maximum size reported in Early Jurassic mammals (Kielan-Jaworowska et al., 2004). This is significant, since burrow dimensions (and especially cross-section size) appear to be tightly controlled by the size (skull width/torso width) of the burrower (e.g., Anderson, 1982; Hickman, 1990; White, 2005; Wilkins and Roberts, 2007). Considering these observations, it appears unlikely that derived therapsids or primitive mammals were the trace makers of the Colonia Ceh Quarry burrows, although their more basal therapsid origin cannot be definitively discarded. Nevertheless, their surprisingly primitive architecture, resembling those from the Permian and Early Triassic in simplicity, is unexpected and considered worth noting (see above).

On the other hand, these tunnels are highly reminiscent of the larger, but more simple burrows described from the Middle Jurassic (Loope, 2008) and Upper Jurassic (Hasiotis et al., 2004) of North America, and referred tentatively to different sauropsid amniotes: to non-specified crocodyliforms, respectively crocodyliforms and/or sphenodontids. Similarities between such burrows and those from Colonia Ceh include the simple morphology consisting of subhorizontal tunnels; circular to subcircular cross-section devoid of a median ridge on the

floor; lengths surpassing 1 m; and large diameters, ranging from 15 to more than 50 cm. However, these tunnels differ from the Romanian burrows in the more vertically sloping inclination of the tunnels, reaching values as high as 22 to 25°, so that the tunnels descend as much as 50 cm into the host sediment instead of being oriented quasi-parallel with the bedding plane.

Nevertheless, neither crocodyliforms, nor sphenodontids should be disregarded as potential trace makers at Anina. Both of these groups are known to have originated in the Late Triassic at the latest (e.g., Benton and Clark, 1988; Evans, 2003) and thus their presence in the Lower Jurassic of the Banat region is definitively conceivable. In fact, despite the general lack of vertebrate body remains from the coal-bearing deposits of the Steierdorf Formation, the presence of indeterminate crocodyliforms was suggested previously, based on the report of tetrapod tracks identified as *Batrachopus* cf. *deweyi* (Hitchcock, 1843) by Popa (2000c). Although the preserved tracks point to a small individual (torso length estimated to about 8–9 cm, width about 7 cm), smaller than the potential trace-maker of the Anina burrows, these tracks attest that crocodyliforms were probable components of the local Early Jurassic palaeoecosystem. Moreover, it is worth noting that Loope (2008) suggested the small-sized Middle Jurassic crocodyliform *Entradasuchus* from the Entrada Sandstone Formation, Utah, to be responsible for the large-scale burrows reported from the same deposits, despite size discrepancies between burrow diameters and estimated body size of *Entradasuchus*. Such a discrepancy would be similar to that existing between the Anina burrows here described and a trace-maker corresponding in dimensions to the *Batrachopus* tracks; furthermore, these tracks are recorded from the basal part of the overlying Valea Tereziei Member, only a few metres higher in section than the burrow-bearing layers (Popa, 2000c). Several small-sized Mesozoic crocodyliforms were suggested to have had burrowing lifestyles based on their preservation style, taphonomic conditions, or presence of supposedly burrowing-related anatomical adaptations, as in the case of *Mala-wisuchus* (Gomani, 1997), *Simosuchus* (Buckley et al., 2000), *Mariliasuchus* (Nobre et al., 2008), *Armadillosuchus* (Marinho and Carvalho, 2009), or *Yacarerani* (Novas et al., 2009). Accordingly, the hypothesis of a crocodyliform trace maker for the Colonia Ceh Quarry burrows is worth considering.

Surprisingly enough, the Colonia Ceh Quarry burrows also show remarkable resemblances to Late Mesozoic burrows attributed to dinosaurs. Although not commonly acknowledged, the presence of digging behaviour or digging adaptations was suggested for different dinosaur taxa based on functional morphology and attributed trace fossils. In many instances, admittedly, these digging adaptations were related not to burrowing, but instead to other behavioural traits such as scratch-digging used in feeding, as was advocated in the case of certain alvarezsaurids (Senter, 2005) and paravialans (Simpson et al., 2010), or in reproduction, as in the case of nest-digging activities reported for hadrosaurs (e.g., Horner, 1982) or titanosaurs (e.g., Vila et al., 2010); nevertheless, true burrowing habit has been also suggested preliminarily by Bakker (1996) for the Late Jurassic basal ornithopod *Drinker*.

Recently, however, burrow structures, represented by relatively simple, subhorizontal tunnels ended by a terminal chamber, have been described from the lower Upper Cretaceous of North America (Varricchio et al., 2007; Woodruff and Varricchio, 2011); these tunnels have a constant, slightly oval cross-section and a slightly descending, sinuous trajectory, being divided along their length (210 cm, as preserved) into 60–70 cm long segments. Such tunnels were referred to the

“hypsilophodontid” – or, more properly, basal neornithischian (Boyd et al., 2009; Boyd, 2015) – dinosaur *Oryctodromeus* based on associated skeletal elements discovered within the terminal chamber. In support of this discovery, the skeletal morphology of this taxon was shown to present digging adaptations (Fearon and Varricchio, 2015), and similar adaptations for limited burrowing were also reported in the basal ornithopod *Koreanosaurus* from the Upper Cretaceous of Korea (Huh et al., 2011). Subsequent to the discovery of the *Oryctodromeus* burrows, structures of similar size and gross morphology were reported from the upper Lower Cretaceous of Australia (Martin, 2009), and were similarly regarded as being produced by basal neornithischians (“hypsilophodontids”), a clade whose representatives are well-represented in contemporary deposits of the same area (Molnar and Galton, 1986; Rich and Vickers-Rich, 1989, 1999). Previously described burrow structures from the Middle Jurassic of North America (Loope, 2006) were already reported to have similar general morphology and dimensions to those reported by Varricchio et al. (2007), and these might hint at an even earlier, pre-Late Jurassic origin of basal neornithischian burrowing habits.

All these tunnel-like structures resemble those from Anina in their relatively large dimensions in length and cross-section (although cross-sectional diameter is somewhat smaller in the Anina burrows), simple subcircular cross-section, and sinuous, gently descending trajectory. They are also isolated tunnels that do not form complex networks, show swells at the turns of tunnels, and can have a roughly parallel trajectory, as was also reported in the case of the Australian burrows described by Martin (2009). Even the presence of occasional branching was described in the case of *Oryctodromeus* burrows by Varricchio et al. (2007).

Comparable dimensions of the burrows suggest similarly sized trace-makers, while their largely analogous morphologies point to similar digging behaviour of these organisms. Considered together, similarities in shape and size would support the hypothesis that the Colonia Ceh Quarry burrows could have been also excavated by basal neornithischian dinosaurs, despite the fact that the structures from Anina look simpler than those from the “mid”-Cretaceous, with chambers that are not present, or at least not recorded in the preserved tunnel segments (Fig. 5A, E), except in one questionable case (burrow no. 4) which, if correctly identified as a terminal chamber, appears to be not connected to tunnels (Fig. 5D).

Members of basal Neornithischia, a phylogenetic position suggested for the trace-makers of the Late Cretaceous North American burrows (and considered as potential trace makers of the Early Cretaceous Australian burrows as well), are known to appear in the Middle Jurassic (Norman et al., 2004). However, the sister-taxon of Neornithischia (i.e., the least-inclusive taxon that includes “hypsilophodontids”) – that is, either Heterodontosauria, according to Norman et al. (2004) or *Thyreophora*, according to Butler et al. (2008; see also Boyd, 2015); as well as basal members of the Neornithischia (*Stormbergia*; Butler et al., 2008) are already known from the Early Jurassic, and these occurrences place the origin of the line leading to “hypsilophodontids” also into the Early Jurassic. And, although dinosaurian body fossils are extremely rare in the Lower Jurassic of Europe, the dinosaurian track record suggests that cursorial ornithischians (even ornithopods) were already present in this area at the beginning of the Jurassic (see Weishampel et al., 2004), including in Central Poland (Gierliński and Piekarski, 1999; Gierliński et al., 2004). It is thus conceivable that basal ornithopods (or basal neornithischians) with a lifestyle similar to that of the members of the later-appearing, burrowing basal

neornithischian clade identified by [Boyd et al. \(2009; Orodrominae of Boyd, 2015\)](#) were also present in the Early Jurassic ecosystem of southwestern Romania, and might be responsible for the burrows reported here.

PALAEOENVIRONMENTAL SIGNIFICANCE OF THE ANINA BURROWS

As reported here, the Hettangian Dealul Budinic Member of the terrestrial Steierdorf Formation, southwestern Romania, yields a record of tetrapod burrows that is unique in the Mesozoic of Romania. These burrows are attributed in this paper either to non-mammalian therapsids, or, more probably, to crocodyliforms or to basal neornithischian dinosaurs with a semi-fossorial habit. Regardless of their exact taxonomic affinity, the precise purpose of digging these burrows remains uncertain, and identification of their purpose depends largely of the identity and ecology of the trace maker. Nevertheless, based on the nature of the published fossil record of tetrapod burrows and on the local geological data, hiding from weather extremes in a terrain influenced by seasonal, periodically harsh conditions, appears to be the most probable explanation for the activity of the trace makers.

Adverse climatic conditions necessitate compensating thermoregulatory behaviour of the organisms, such as usage of diurnal shelter, thus we suggest as a working hypothesis a significant climatic control on the burrowing behaviour of Early Jurassic Romanian tetrapods. Indeed, many Early Mesozoic fossil vertebrate burrows have been discovered from strata that document extremes in global palaeoclimatic fluctuations (e.g., [Smith, 1987, 1995; Damiani et al., 2003; Smith and Botha, 2005; Abdala et al., 2006](#)). Meanwhile, other burrows originated in palaeoenvironments marked by seasonally harsh, extreme conditions such as severe aridity (e.g., [Voigt et al., 2011; Krapovickas et al., 2013](#)) or prolonged cold periods (e.g., [Martin, 2009](#)).

Based on these cases, all of which document strong environmental (i.e. climatic) control on the presence of burrowing habits, it can be hypothesized that their fossorial behaviour allowed trace makers of the Anina burrows to ameliorate the strongly seasonal climatic conditions of the earliest Jurassic, as were the ones suggested by the local sedimentary record. It is well-constrained based on phytostratigraphy that the Dealul Budinic Member of the Steierdorf Formation was deposited during the earliest Jurassic or near to the Triassic/Jurassic transition, and is thus close to the Triassic/Jurassic boundary extinction event. Furthermore, sedimentological features of the Steierdorf Formation suggest that the burrows were made in a period of increased aridity corresponding to the depositional time of the Dealul Budinic Member, preceding the onset of

milder, more humid climates suggested by the coal-bearing beds of the Valea Tereziei Member. Similarly to the case of the Permian/Triassic boundary, when high abundance of burrowing tetrapods is recorded in the aftermath of the extinction event ([Smith and Botha, 2005; Bordy et al., 2011; Viglietti et al., 2013](#)), the times around the Triassic/Jurassic boundary event appear to be also marked by changing seasonal climate with prolonged droughts and extreme moisture and temperature fluctuations. It may be thus stipulated that within the first million year interval following the Triassic/Jurassic boundary event and under adverse environmental conditions, fossorial habit probably became yet again an endurance strategy for the burrow makers such as those whose activity is recorded in the Lower Jurassic deposits of Anina.

CONCLUSIONS

The terrestrial Steierdorf Formation of Early Jurassic (Hettangian–Sinemurian) age from the Re ita Basin, in the South Carpathians, Romania, a highly significant for its well-preserved and diverse plant fossil record, as well as its recently identified terrestrial trace fossils. More specifically, the lower unit of the Steierdorf Formation, the Hettangian Dealul Budinic Member, yields tetrapod burrows that are unique for the Mesozoic of Romania as well as for the Lower Jurassic of Europe. Based on their size, morphology and pattern of development, these burrows are attributed in this paper either to non-mammalian therapsids, or, more probably, to small-sized crocodyliforms or basal neornithischian dinosaurs with a semi-fossorial habit. Although the exact purpose of these burrows remains uncertain, it can be hypothesized that they contributed to the success of the survival strategy employed by the trace maker organisms in coping with the seasonally arid environmental conditions that characterized – according to the local sedimentological record – the first few million years following the Triassic/Jurassic boundary extinction event, that is, the time of deposition of the burrow-bearing Dealul Budinic Member.

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