The ichnospecies *Tambia gregaria* (Fritsch, 1908) comb. nov. from the Upper Ordovician of Czechia

Dirk Knaust, Radek Mikuláš, M. Gabriela Mángano,
Renata Netto & Luis A. Buatois

The trace fossil *Curvolithus gregarius* Fritsch, 1908 was introduced for curved and scratched burrows at the base of sandstone beds formed in storm-dominated environments recorded in the Upper Ordovician Kosov Formation in Czechia. Given its morphological difference with *Curvolithus multiplex* Fritsch, 1908, the type ichnospecies of *Curvolithus*, *C. gregarius* is transferred to the ichnogenus *Tambia* Müller, 1969 as *Tambia gregaria* comb. nov. This crescent-shaped burrow contains sets of robust, rarely overlapping scratches, suggesting an arthropod producer. It is commonly closely associated with elongate cylindrical burrows, which partly have an active backfill. Potential behavioural interpretations are discussed, but the available evidence is still insufficient. • Key words: trace fossil, arthropod burrow, *Tambia*, *Curvolithus*, Ordovician, Czechia, behaviour.

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Dirk Knaust, Equinor ASA, 4035, Stavanger, Norway; dkna@equinor.com • Radek Mikuláš, Institute of Geology of the Czech Academy of Sciences, Praha, Czech Republic • M. Gabriela Mángano & Luis A. Buatois, Department of Geological Sciences, University of Saskatchewan, 114 Science Place, Saskatoon, SK S7N 5E2, Canada • Renata Netto, ICHNOS Research Group, Geology Graduate Program, Unisinos University, Av. Unisinos, 950, 93022-000, São Leopoldo, RS, Brazil

Trace fossils are invaluable for palaeoenvironmental reconstructions (*e.g.* Pemberton 1992, Pemberton *et al*. 2001, Buatois & Mángano 2011, Knaust & Bromley 2012) and for detecting evolutionary trends (*e.g.* Mángano & Buatois 2016a, b). Increased interest in ichnology resulted in the description and erection of numerous ichnotaxa that allowed for their recurrent recognition and communication. However, after the compilation of the second edition of the *Trace Fossils* volume in the *Treatise of Invertebrate Paleontology* (Häntzschel 1975), the number of valid invertebrate ichnogenera has multiplied (Knaust 2012, Buatois *et al*. 2017). Many ichnotaxa are based on weak grounds, either due to inappropriate characteristics chosen as ichnotaxobases, poor preservation, single specimens, or simply overlooked synonymy. Accordingly, comprehensive ichnotaxonomic reciews are necessary for the efficient and robust application of ichnologic evidence.

This contribution provides a taxonomic assessment of the ichnospecies *Curvolithus gregarius* Fritsch, 1908 from the Upper Ordovician of Czechia (see Mikuláš 1992, for previous evaluations of this ichnofauna), based on a reinvestigation of the type material and newly collected specimens. In a general review of the ichnogenus *Curvolithus*, Buatois *et al*. (1998) excluded the ichnospecies *C. gregarius* from that ichnogenus due to the morphological discrepancy with the diagnostic features of *Curvolithus*. These authors also noted similarities of the type material of *C. gregarius* with other scratched trace fossils supposedly produced by arthropods, such as *Tambia* and *Monomorphichnus*. However, no formal ichnotaxonomic decision was made at that time, and the ichnotaxonomic status of this ichnospecies was left indeterminate.

Here, we formally include *C. gregarius* in *Tambia* Müller, 1969 as *T. gregaria* comb. nov. In addition, we briefly revise other ichnotaxa described by Fritsch (1908) that are related to *T. gregaria*. This study is part of an overall examination of historical trace-fossil collections and ichnotaxonomic re-evaluation of the collection of Fritsch (1908) at the National Museum in Prague, Czechia.

Geologic setting

The uppermost Ordovician (Hirnantian) Kosov Formation (*e.g.* Brenchley & Štorch 1989) is exposed in the Prague Basin and in the Rožmitál Trench (*e.g.* Mikuláš 1995; Fig. 1A, B). Both regional geological units belong to the

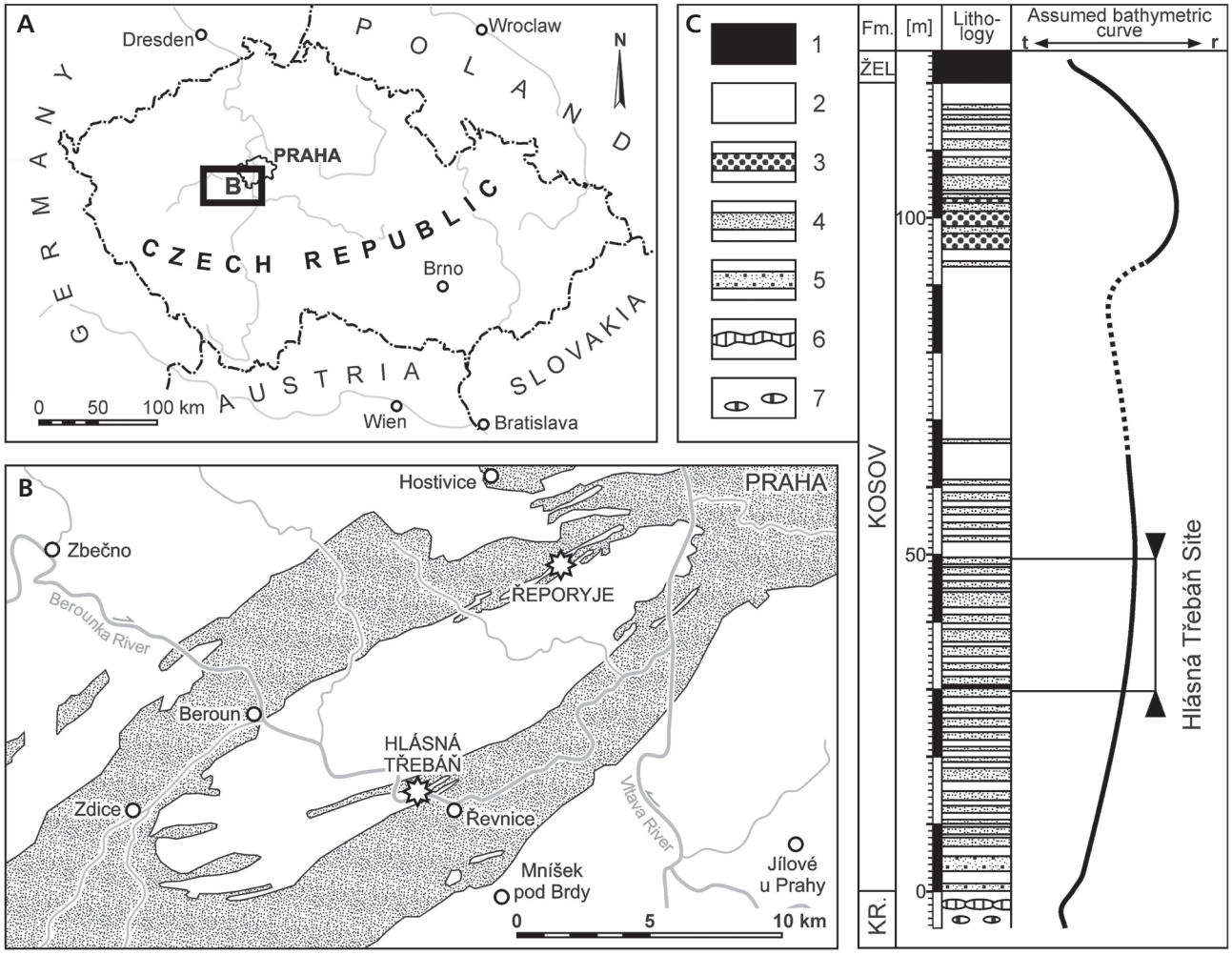

Figure 1. Location map and stratigraphy (modified after Mikuláš 1992). • A – Czech Republic and neighbouring countries with location of inset map in B. • B – map displaying outcrops of Ordovician age (stippled) in the Prague Basin. • C – generalized section of the Kosov Formation. Lithology and bathymetry after Štorch (1986, 1990). Legend:1 – Graptolitic shale; 2 – claystone and siltstone; 3 – coarse- to very coarse-grained sandstone and conglomerate; 4 – very fine- to medium-grained sandstone; 5 – coarse-grained wacke; 6 – clayey limestone; 7 – limestone concretions and lenses; Fm. – Formation; ŽEL. – Želkovice; KR. – Králův Dvůr; t – transgression; r – regression.

Bohemian Massif, which covers areas of Czechia, eastern Germany, southern Poland, and northern Austria. More than half of the Bohemian Massif consists of crystalline rocks are older than Carboniferous and therefore were deformed during the Variscan Orogeny (*e.g.* Havlíček 1998). The Prague Basin represents a major part of the so-called Barrandian area, well known for its rich fossil content. During the 19th century, the richness of middle Cambrian and Lower Ordovician–Middle Devonian fossils allowed the French palaeontologist Joachim Barrande to write the yet largest scientific volume written by a single person (Barrande 1852–1883, Barrande *et al.* 1852–1911).

The Variscan Orogeny was a phase of mountain building and accretion of terranes that resulted from the closure of the Rheic Ocean, when the two palaeocontinents Gondwana (in the south) and Laurussia (in the north) collided. The good preservation of Palaeozoic fossils in the Bohemian Massif can be explained by the existence of the microcontinent Perunica, which represented the Precambrian core of the Bohemian Massif. As a result, the Lower Palaeozoic rocks could rest in the overburden of the Neoproterozoic volcanic-sedimentary rocks and were not metamorphosed during the Gondwana-Laurussia collision (Havlíček *et al*. 1994). The existence of Perunica, however, is not generally accepted (Fatka & Mergl 2009). During the Variscan Orogeny, almost all continental mass was united in the supercontinent Pangaea (Scotese 2021). Since the end of the Palaeozoic, the Variscan mountain belt became eroded and partly covered with younger sediments.

The Kosov Formation mostly consists of alternating green-greyish sandstone and micaceous shale (*e.g.* Brenchley & Štorch 1989; Fig. 1C). It contains two layers of coarse-grained wacke at its base, interpreted as glacial-

marine deposits (diamictites; Brenchley & Štorch 1989, Štorch 1990). The remaining part of the formation bears structures typical of storm deposition, such as hummocky-cross stratification, observed at Řeporyje, Hlásná Třebaň and other localities (Brenchley & Štorch 1989, Buatois *et al*. 1998). Although its body-fossil record is quite poor (except for its lowermost and uppermost layers, *e.g.* Marek & Havlíček 1967, Havlíček 1982 and Mergl 2011), the Kosov Formation hosts a rich ichnofauna, including *Asteriacites*, *Bifungites*, *Cruziana*, *Curvolithus*, *Dimorphichnus*, *Diplichnites*, *Fustiglyphus*, *Monofungites*, *Monomorphichnus*, *Planolites* and *Rhizocorallium* (*e.g.* Mikuláš 1992).

The trace fossil described by Fritsch as *Curvolithus gregarius* is common at the Hlásná Třebaň locality (Mikuláš 2019). The name of the site (then Vorder Třebaň, meaning Front Třebaň) appeared in the "*Problematica Silurica*" by A. Fritsch in 1908. Since then, the site has been sporadically mentioned in explanations to geologic maps. Furthermore, it is described in more detail in the sedimentological study by Bouček & Přibyl (1958), by Brenchley & Štorch (1989) from the Hlásná Třebaň II section, in the work of Mikuláš (1992), and a recent field guide (Mikuláš 2019). Further individual specimens assigned to *C. gregarius* were recorded from Řeporyje (Fig. 1) and Levín localities (Mikuláš 1992). Poorly preserved specimens with similarities to *C. gregarius* were also found in the Letná Formation (Sandbian) of the Prague Basin.

The Hlásná Třebaň site is on the southern slope of a prominent mountain ridge with poor vegetation and thus containing numerous and relatively large outcrops. The whole area suitable for the study of the Kosov Formation is *ca*. 30 × 300 m. This slope is partly terraced, probably due to its historical use for the cultivation of grapevine (local name Vinice, meaning 'vineyard'). The Kosov Formation in this section comprises a coarsening-upward succession, which in turn can be subdivided into a series of small-scale coarsening-upward intervals. The stratal stacking pattern is interpreted as a series of dis-

Figure 2. Lectotype of *Tambia gregaria* (Fritsch, 1908) comb. nov. (hyporelief preservation) from the Upper Ordovician Kosov Formation of Hlásná Třebaň, southwest of Prague, Czechia. The sample contains three partly overlapping clusters of burrows. The white staining was originally done to highlight the burrows from their background. L 7536; A – original label; B – overview of the slab showing three clusters of burrows, each consisting of a group of individual bow-shaped burrows that are crosscut by an elongate horizontal burrow (white arrows). The herein defined lectotype is indicated (black arrow), while the remaining specimens of that sample constitute paralectotypes; C – close-up of the main cluster illustrated in B; D – close up of the lectotype. Note the strong subparallel scratches and local criss-crossing in the paratype on the right. Scale bars = 1 cm.

crete parasequences forming a single progradation parasequence set. A transgressive deposit is present at the top of the parasequence set as part of the so-called "lower flysch" of alternating storm sandstone beds and shale in the sense of Brenchley & Štorch (1989), Štorch (1990), Brenchley *et al*. (1991) and Štorch (2006).

Two main sedimentary facies are observed: (1) regularly interbedded hummocky cross-stratified and wave-ripple cross-laminated, very fine-grained sandstone and shale; and (2) amalgamated hummocky cross-stratified,very fine-grained sandstone. Some sandstone layers bear prominent, sharp tool marks on their bases (Fig. 1C). Soft-sediment deformation structures, such as ball-and-pillow structures, are present locally. While the amalgamated sandstone beds are generally poor in trace fossils, the discrete hummocky cross-stratified sandstone layers contain relatively rich trace-fossil assemblages preserved in hyporelief and epirelief (*Rusophycus* isp., *Cruziana problematica*, *Asteriacites* isp., *Helminthoidichnites* isp., *Bifungites* isp.; Mikuláš 2019).

The succession represents deposition in a wave-dominated, shallow-marine setting. The interbedded sandstone and shale record the alternation of storm events and fair-weather suspension fallout in offshore to offshore-transition environments, between the storm-wave base and the fair-weather wave base. These most distal deposits of the Kosov Formation host the diverse trace-fossil assemblage as previously outlined, including *Tambia gregaria* as analyzed in this contribution. The amalgamated sandstone beds, mostly devoid of biogenic sedimentary structures, represent repeated storm erosion and deposition events in a lower to middle shoreface above the fair-weather wave base.

Systematic ichnology

Institutional abbreviations. – GST – Geological Survey of Thuringia, Jena/Weimar, Germany; L – National Museum Prague, Czech Republic; MB.W – Palaeontological Collection of the Museum of Natural History, Berlin, Germany; P – Phyletic Museum Jena, Germany.

Ichnogenus *Tambia* Müller, 1969

Type ichnospecies. – *Tambia spiralis* Müller, 1969.

Diagnosis. – Original: Screwed-in semireliefs or flat structures with a rounded outline. The surface is covered by fan-shaped or parallel to the outer edge running striae [translated from German].

Revised: Shallow vertical, inclined to horizontal burrows with a semi-circular, circular, crescentic, or spiral shape, covered with sets of parallel striae.

Remarks. – The ichnogenus *Tambia* was established for heavily scratched burrows with a circular or spiral-like outline from the lower Permian (Cisuralian) Tambach Formation of Germany. This ichnotaxon is preserved at the base of sheet sandstone of alluvial origin (Eberth *et al*. 2000) and displays high morphological variability (Müller 1956, Martens 1975). It occurs in close association with *Scoyenia gracilis* White, 1929 and another ichnotaxon of scratch imprints, *Striatichnium bromackerense* Martens, 1982, as well as various tetrapod trackways. *Tambia spiralis* was originally interpreted as the surface trace of an arthropod or annelid (Müller 1954), although the sharp scratches indicate the action of robust appendages, thus suggesting production by arthropods.

Ichnospecies *Tambia gregaria* (Fritsch, 1908) comb. nov.
Figures 2, 4–6

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*1908 *Curvolithus gregarious*; Fritsch, pp. 13, 14, fig. 1.

Types. – L 7536 (Fig. 2A–D). One sample from Hlásná Třebaň with several clusters of burrows was figured in the original publication by Fritsch (1908), of which "… a group of furrows" was referred to as lectotype by Mikuláš (1992, p. 31, pl. 15, fig. 5). Since this cluster consists of several partially superimposed burrows, a single burrow is herein defined as the lectotype of *T. gregaria* in accordance with Article 74 of the ICZN

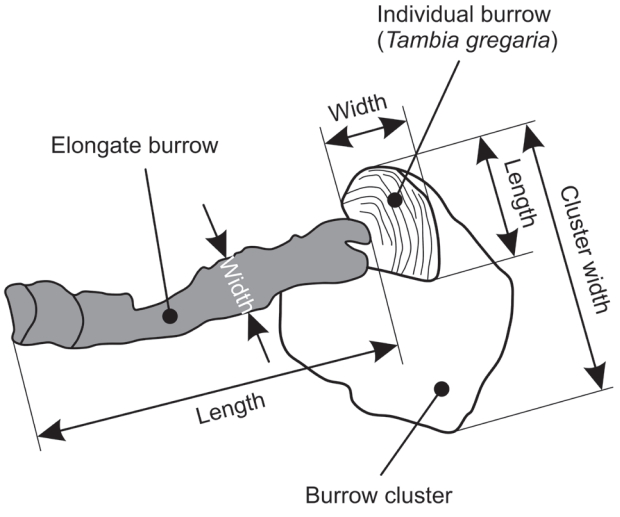

Figure 3. Sketch, based on the lectotype sample (see Fig. 2B), to illustrate the applied terminology and description in the text. The diagnosis of *Tambia gregaria* comb. nov. includes individual burrows, but not burrow clusters or the associated elongate burrow.

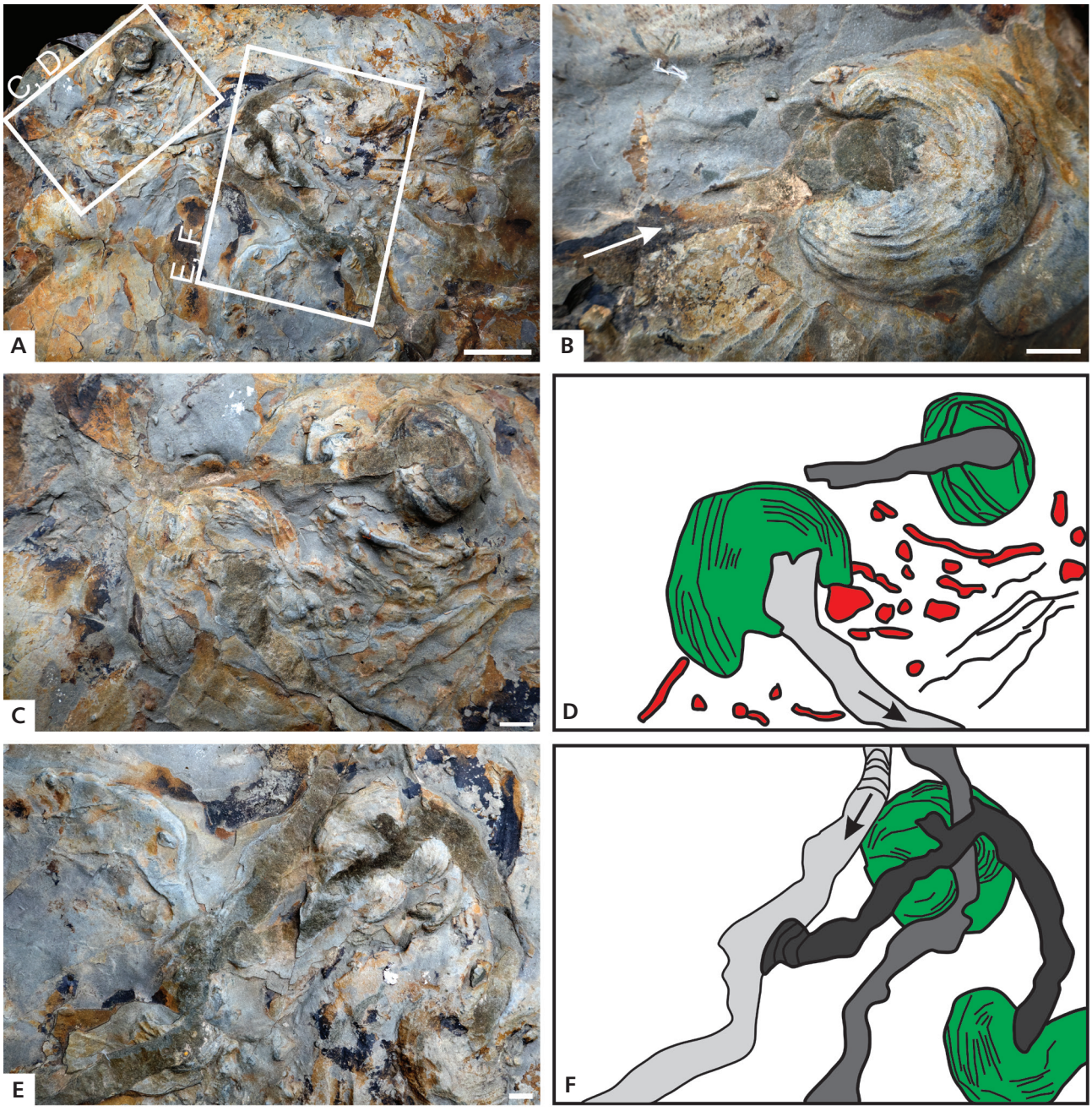

Figure 4. Lower sandstone bedding plane with several specimens of *Tambia gregaria* (Fritsch, 1908) comb. nov. (hyporelief preservation) from the Upper Ordovician Kosov Formation of Hlásná Třebaň, southwest of Prague, Czechia. L 53292. A – overview with several *T. gregaria* and associated elongate horizontal burrows. B – semi-circular, slightly spiral *T. gregaria* with longitudinal scratches and cross-cutting elongate burrow (arrow). C – two specimens with horizontal burrows and associated bioturbation. D – interpretative and simplified line drawing of C showing *T. gregaria* (green), elongate burrows (grey) and shallower traces (red). The arrow indicates continuation of burrow in F. E – two specimens with cross-cutting elongate tunnels, some of which show meniscate backfill. F – interpretative and simplified line drawing of E showing *T. gregaria* (green) and elongate burrows (shades of grey). The arrow indicates continuation of burrow from D. Scale bars = 5 cm (A) and 1 cm (B–D).

(1999; Fig. 2B, black arrow), and all remaining similarly scratched burrows constitute paralectotypes.

Type horizon and locality. – Kosov Formation (Hirnantian, Upper Ordovician); Hlásná Třebaň, southwest of Prague, Czechia.

Material. – Types and nine additional samples containing 13 individual burrows and one cluster of three burrows were studied (Tab. 1).

Diagnosis. – Original: Fossils in relief, which affect the short and long *Bilobites* shape. The largest of them have

Table 1. Studied material of *Tambia gregaria* (Fritsch, 1908) comb. nov.

Inv. No.	Locality	Original name	Reference	Figure	Number of clusters	Number of individual burrows
L 7536	Hlásná Třebaň	*Curvolithus gregarius*	Fritsch (1908, fig. 1)	2	3	14
L 7768	Hlásná Třebaň	Fucoid	Fritsch (1908, fig. 7)		1	1
L 7816	Radotín	*Crossochorda* sp.	Fritsch (1908, pl. 10, fig. 5)		1	1
L 27726	Řeporyje	*Crossochorda* sp.	Fritsch?		1	1
L 59792	Braník	*Crossochorda* sp.	Coll. 19th century, not studied by Fritsch		1	1
L 59790	Řeporyje		Coll. 19th century, not studied by Fritsch	6A	1	1
L 52025	Řeporyje		Coll. 19th century, not studied by Fritsch		1	3
L 59791	Řeporyje		Coll. 19th century, not studied by Fritsch		1	1
L 52024	Hlásná Třebaň	*Rusophycus*? isp.	Mikuláš (2019, fig. 6)	5B	1	1
L 53292	Hlásná Třebaň	*Tambia gregaria*	Mikuláš, coll. in 2020	4, 5A, 8	6	6

a length of 30 cm and a width up to 15 cm. They are curved and have seven protruding and smooth, longitudinal ribs. From the group stands a Fucoid and a short extension, ear-shaped [translated from French].

Revised: Horizontal to inclined, crescent-shaped, passively filled burrows with sets of longitudinal, sub-parallel or rarely crossing striae. Burrows occur isolated or forming irregular clusters of partially overlapping specimens.

Description. – Fritsch's original slab including the lectotype specimen contains three clusters with a total of 14 individual, arcuate burrows displaying variable convexity at the base (*i.e.* positive hyporelief, Fig. 2A–D; for terminology, see Fig. 3). The clusters are irregular in morphology, partly overlapping, and contain two to ten burrows that tend to display similar general orientation (*i.e.* the convexity of crescentic structures in the same direction). Individual burrows are 2.7–6.0 cm in length, up to 1.9 cm in width, and oriented obliquely to the bedding (*ca.* 10–30°). Burrows are deeply ornamented with a dense system of strong scratches that mainly run in longitudinal direction, rarely diverging (*i.e.* bifurcating) or cross-cutting each other. Thick striae, 0.2–0.3 cm wide, constitute the dominant ornamentation, but a few specimens exhibit thinner sub-parallel striae typically occurring in the shallower part of the burrow (*i.e*. adjacent to the surface of the sandstone bed). The lectotype is 2.7 cm long, 1.9 cm wide, and *ca*. 20° inclined to the bedding (Fig. 2B–D). It contains up to nine longitudinal scratches separated from each other by *ca*. 0.1–0.2 cm. Additional specimens of *T. gregaria* in Fritsch's collected slabs consist of burrows with a bow-shaped to semi-circular outline also forming irregular clusters (Figs 4–6). Some isolated specimens, such as L 52024 (Fig. 5B) and, to a lesser degree, L 59790 (Fig. 6A), show an almost circular outline.

Remarks. – *Curvolithus* Fritsch, 1908 was erected for "… curved, short, conical remains, whose surface is decorated with many furrows" occurring in the Ordovician of Czechia. The diagnosis of *Curvolithus* was subsequently revised to include "straight to curved, horizontal, sub-horizontal to rarely oblique, ribbonlike or tongue-like, flattened...traces with three rounded lobes on upper surface", in alignment with the common understanding of this ichnotaxon (Buatois *et al*. 1998). The type material of Fritsch's two ichnospecies, *C. multiplex* and *C. gregarius*, differs significantly in morphology (Buatois *et al*. 1998). *Curvolithus multiplex* was subsequently designated as the type ichnospecies of *Curvolithus* by Häntzschel (1962), whereas *C. gregarius* was removed from *Curvolithus* due to the lack of the diagnostic three-lobe morphology (Buatois *et al*. 1998). Similarities of *C. gregarius* with *Monomorphichnus* Crimes, 1970 and *Tambia* Müller, 1969 were noted by Buatois *et al*. (1998).

The characteristic morphology and scratches of *C. gregarius* make this ichnospecies similar to other ichnotaxa, most notably the oblique U-shaped spreite burrow *Rhizocorallium jenense* Zenker, 1836 and *Gyrolithes polonicus* Fedonkin, 1981 (Fig. 7). In contrast to *Rhizocorallium*, there is no clear evidence of a causative U-shaped burrow and spreite in *C. gregarius* (see Fürsich 1974 and Knaust 2013). The diagnostic spiral architecture of *Gyrolithes polonicus* is not evident in *C. gregarius* (see Uchman & Hanken 2013, Laing *et al.* 2018). *Monomorphichnus* is a problematic ichnogenus comprising a set of

Figure 5. Specimens of *Tambia gregaria* (Fritsch, 1908) comb. nov. (hyporelief preservation) from the Upper Ordovician Kosov Formation of Hlásná Třebaň, southwest of Prague, Czechia. A – partly broken, oblique specimen exposed together with a shallower elongate burrow (arrow). L 53292 B. B – semi-circular specimen crosscut with a short, steeply inclined tunnel (arrow). L 52024. C – bow-shaped, oblique specimen crosscut by two undulating burrows (arrows). Field photograph. Scale bars = 1 cm.

simple scratch imprints (Crimes 1970, but see Seilacher 1985), whereas *C. gregarius* is a scratched burrow.

This study proposes transferring *C. gregarius* to the ichnogenus *Tambia*, as a separate ichnospecies. For a correct declination of the ichnospecies name concerning its new ichnogenus name, the nomen *gregarius* has been corrected to *gregaria*. *Tambia gregaria* differs from *T. spiralis* by having a strong crescentic shape instead of a spiral or

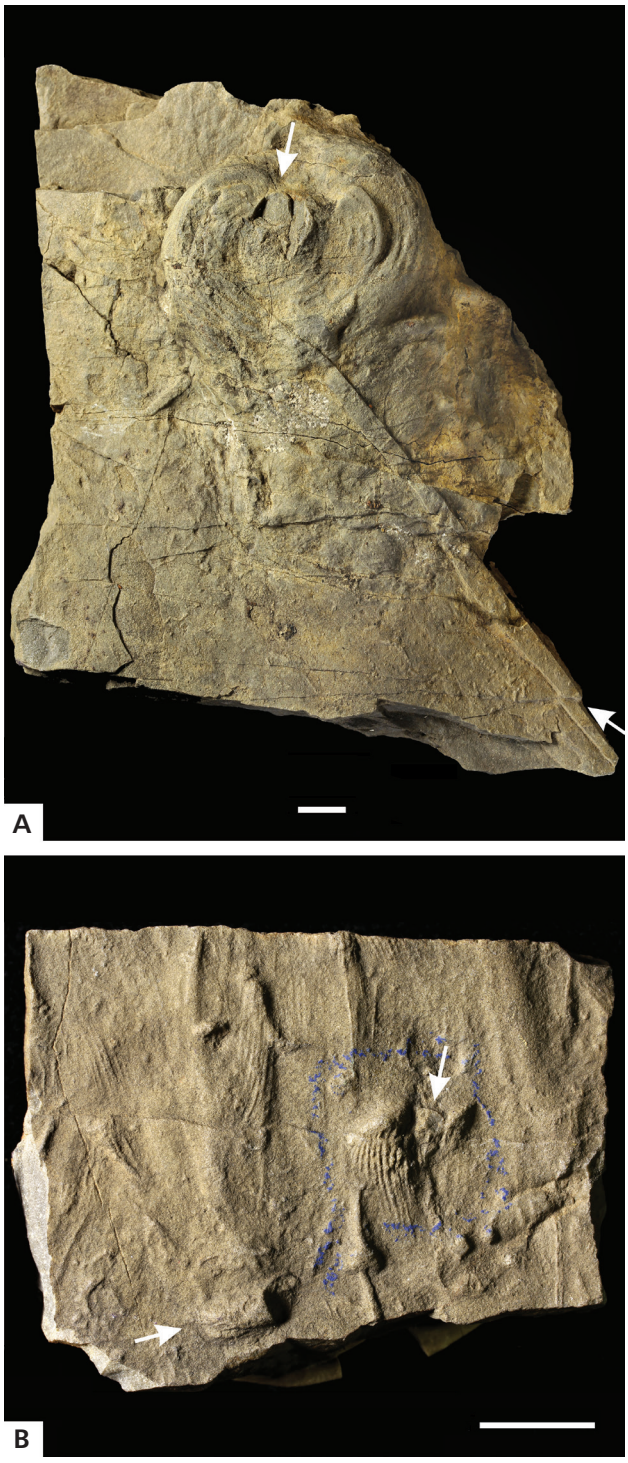

Figure 6. Specimens from the Fritsch collection with *Tambia gregaria* (Fritsch, 1908) comb. nov. and associated traces and structures from the Upper Ordovician Kosov Formation of Hlásná Třebaň, southwest of Prague, Czechia. A – semi-circular specimen with longitudinal scratches and a long elongate structure cross-cutting into it (arrowhead), while an elongate burrow crosscuts the inner part of *Tambia gregaria* in a subvertical direction (arrow). L 59790. B – tool marks and longitudinally scratched burrows at the base of a sandstone bed together with subvertically penetrating tunnels (arrows). Original from Fritsch (1908, pl. 10, fig. 4), labelled as *Pattes natatoires*. L 27728. Scale bars = 1 cm.

circular outline, and mainly longitudinal subparallel striae instead of fan-shaped striae arranged in a spiral fashion (Fig. 7A, B). Moreover, *T. gregaria* tends to build clusters of partly overprinting burrows, a feature rather unknown from commonly single *T. spiralis*.

Sandstone slabs with scratched burrows are common in Fritsch's collection of trace fossils from the Kosov Formation. Some of these trace fossils described and figured by Fritsch (1908) deserve further discussion due to their similarities with *T. gregaria* to explore potential synonymies. Two specimens referred to as *Crossochorda* isp. were figured by Fritsch (pl. 12, fig. 13 and pl. 10, fig. 5). These consist of burrows with a series of arch-shaped scratch imprints. *Crossochorda* Schimper, 1879 *in* Schimper & Schenk (1879) is a poorly known ichnogenus that Häntzschel (1975) regarded as a junior synonym of *Crossopodia* M'Coy, 1851. However, this ichnogenus has a convoluted history (see discussion in Mángano *et al*. 2002) and its use is not recommended. In fact, *Crossochorda* may be a junior synonym of *Protovirgularia* or *Cruziana* (Mángano *et al*. 2002). In any case, these two specimens of *Crossochorda* isp. figured by Fritsch (1908) do not display the diagnostic features of any of these ichnotaxa and are better accommodated in *T. gregaria* based on their overall morphology and typical scratch patterns.

Another specimen was figured by Fritsch (pl. 9, fig. 3) as *Crossopodia costata*? However, this specimen shows some scratches with a higher curvature than typical for *T. gregaria*. In addition, this burrow is U-shaped and contains a spreite, therefore better assigned to *Rhizocorallium commune*.

A single specimen of the ichnotaxon *Digitolithus rugatus* (Fritsch 1908, fig. 7; see Knaust 2020) contains an arched burrow with scratches closely resembling some occurrences of *T. gregaria*. *Alectorurus venosus*, as illustrated by Fritsch (1908, pl. 3, fig. 8), shows a lobate structure with scratches, although in this case, affinity with *T. gregaria* is more debatable.

Finally, longitudinally scratched burrows commonly occur together with tool marks at the base of sandstone beds (L 27728, Fig. 6B; originally labelled as *Pattes natatoires* by Fritsch 1908, pl. 10, fig. 4), for instance in some localities of the Kosov Formation (*e.g.* Levín). They resemble incompletely preserved (*e.g.* partly eroded) burrows and are a preservation variant of *T. gregaria*.

Tambia gregaria is associated with elongate burrows, up to 13 cm long and 0.5–1.6 cm wide, which, in some cases, seem to emerge from the concave part of the arcuate burrows (Figs 4C, D; 8), crosscut it in others (Fig. 4E, F), and occur in the area of highest convexity in some situations (Fig. 5B, C). These elongate burrows display a very irregular morphology with an undulating outline or appear as angular and kinked. Terminal expansions are

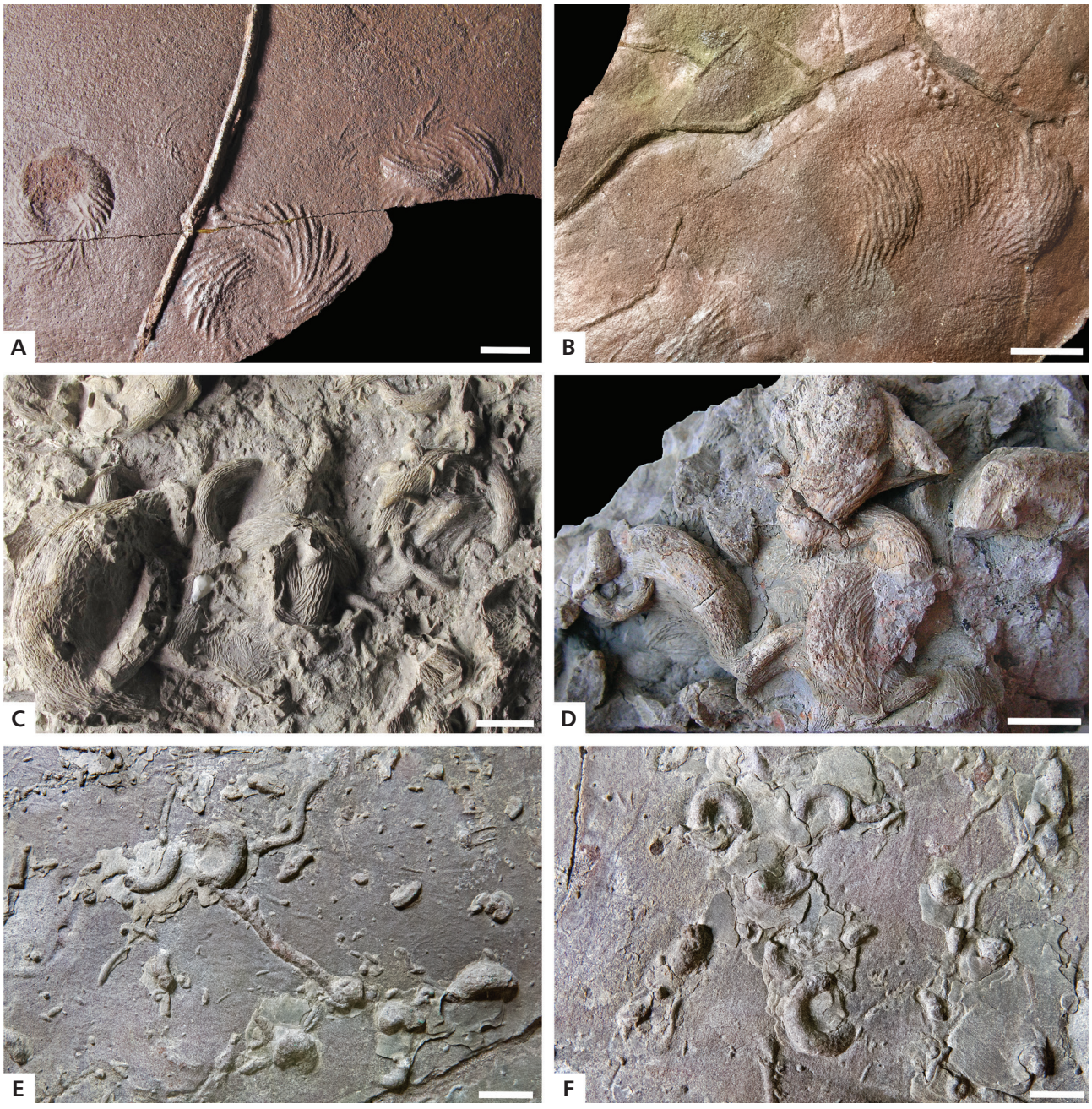

Figure 7. Scratched burrows of different ichnotaxa with similar morphology as *Tambia gregaria* comb. nov., preserved in hyporelief. • A, B – *Tambia spiralis* Müller, 1969, at the base of alluvial sandstone on top of mudstone with desiccation cracks. Permian (Rotliegend) Tambach Formation, Bromacker near Tambach-Dietharz, Germany. P 555 (A), MB.W 25 (B). • C, D – *Rhizocorallium jenense* Zenker, 1836 from the Röt Formation of Jena, Germany. GST 5035-701-202 (C, coll. K. Mägdefrau) and P 1821 (D). • E, F – *Gyrolithes polonicus* Fedonkin, 1981 (= *Spiroscolex spiralis* Torell, 1870) from the lower Cambrian Mickwitzia Sandstone of Lugnås, southern Sweden. MB.W 1829. Scale bars = 1 cm.

common. The local presence of rough menisci suggests active fill with sediment slightly different from the host sediment. In particular, the lectotype of *T. gregaria* is associated with an 8.4 cm long and 0.7–1.6 cm wide horizontal burrow with a bulbous outline (Fig. 2B). Weak annulation and rough menisci are poorly developed in parts of the elongate burrow. Some elongate burrows in other slabs are slightly inclined (up to *ca*. 20°), dipping away from *T. gregaria* (Figs 2B–D, 5A). In specimens L 52024 (Fig. 5B) and L 59790, a short, steeply inclined burrow crosses the burrow apex. In addition, an elongate, shallow, gently tapering, roughly straight burrow, 4.8 cm long and 4.0–4.5 cm wide, is associated with the specimen of *T. gregaria* in L 59790 (Fig. 6A).

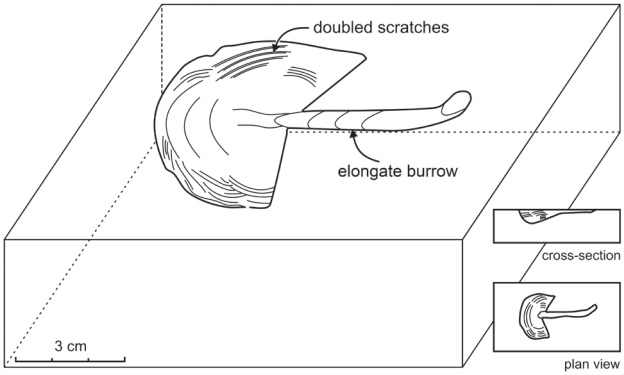

Figure 8. Idealized reconstruction of *Tambia gregaria* and the associated elongate burrow, based on specimen L 53292 D (Fig. 4C).

Discussion

The ichnogenus *Tambia* was originally interpreted as the surface trace of annelids or arthropods (Müller 1954). Both groups of organisms can generate scratch imprints in cohesive substrate during excavation, but only arthropods tend to produce deep, robust striations due to the action of articulated appendages. However, conspicuous, subparallel striae have also been described as ornamentation in some burrows produced by the priapulid *Priapulus caudatus* (see Kesidis *et al*. 2019). In addition, more localized striation has been noted in *Treptichnus rectangularis* by Orłowski & Żylińska (1996). These authors attributed the striation to spines, highlighting their presence in the proboscis of priapulids. Subsequent work interpreted this striation as produced by the scalids that are organized forming a ring in priapulids, based on similarities in number (20) and overall characteristics (Kesidis *et al.* 2019). However, the mostly parallel, local crisscrossing of the striae in *T. gregaria* militates against a priapulid producer. In short, the prominent ornamentation of *T. gregaria* suggests arthropods rather than priapulids or annelids as potential trace makers.

Different groups of arthropods may have been able to produce *T. gregaria*. Trilobites were common components in lower Palaeozoic shallow-marine settings. In the Kosov Formation, trilobites and other body fossils are very rare, except in the uppermost layers containing the so-called Hirnantia fauna. This scarcity of body fossils seems to be related to taphonomic processes instead of original absence (Havlíček 1998). Mikuláš (1992) studied trace fossils of the Kosov Formation and found several ichnotaxa attributable to trilobites or other arthropods, including *Cruziana*, *Dimorphichnus*, *Diplichnites* and *Monomorphichnus*. Notably, *T. gregaria* does not show morphologic features typical for trilobite trace fossils. Moreover, the dominantly sub-parallel striae along the axis of the burrow seem to be incompatible with the metachronal movement of multiple-legged trilobites that typically produces discrete, multiple striae and criss-crossing patterns.

Early representatives of the Malacostraca, such as some phyllocarids, have been hypothesized to have had an infaunal mode of life (Collette & Hagadorn 2010) and could be potential producers. Although criss-crossing is only locally present, this pattern could be consistent with the combined lateral (produced by thoracic appendages) and frontal strokes (produced by head appendages) of phyllocarid crustaceans.

The robust scratches of *T. gregaria* suggest excavation of a cohesive, firm, muddy substrate by the action of strong appendages. Firmground burrows commonly remain open for a while after their abandonment and burrow maintenance may have been involved to keep the structures open. Open burrows are subsequently passively filled, for instance during transgressions or storm events (*e.g.* Tedesco & Wanless 1991). *T. gregaria* is preserved at the base of tempestites and is not associated with any surface bearing allostratigraphic significance. Accordingly, the formation of a firm surface was most likely due to storm erosion related to autogenic processes.

Reconstructing the behavioural significance of these scratched burrows is not straightforward. Vigorous use of appendages during scratching may serve various purposes, including most notably different feeding strategies (*e.g.* microbial grazing, predation) and moulting. Microbial grazing is hard to invoke as no evidence of microbial mats (*e.g.* microbially induced sedimentary structures) is apparent in the studied surfaces. In addition, the highly convex arcuate burrow morphology and penetrative nature do not seem to be consistent with microbial grazing.

Predation may be suggested based on a common association with horizontal burrows, in a fashion like *Rusophycus* produced by trilobites hunting for worms, such as *Planolites*, *Helminthopsis* and *Teichichnus* (Jensen 1990, Pickerill & Blissett 1999, Tarhan *et al*. 2012). However, in the case of the association of *T. gregaria* with the prominent elongate burrows, the latter clearly crosscut the former, indicating their subsequent origin (*i.e.* after the formation of *T. gregaria*). The morphology of these long, horizontal burrows and their relation to *T. gregaria* remain enigmatic.

These structures present drastic, sharp kinks and turns that are more akin to a relatively compacted sediment (*i.e.* firm); however, the infill of these structures, changes in burrow width, and bulgy boundaries suggest a poorly consolidated sediment infill that contrasts remarkably with the firm substrate of *T. gregaria*, suggesting a post-depositional softground suite.

Finally, organisms rid themselves of the exuvia during moulting by thrashing about, twisting around, or rubbing themselves against the sediment (Vallon *et al*. 2015).

These processes may result in well-defined scratch imprints. However, moulting behaviour is implausible in the case of *T. gregaria*, whose producer seems to record the active use of appendages for excavation.

To sum up, the co-occurrence of *T. gregaria* and the elongate horizontal burrows may reflect the reuse of some resources in previously produced structures (*i.e. T. gregaria*). Still, a clear genetic link between both traces cannot be supported based on available morphologic evidence.

Conclusion

Curvolithus gregarius Fritsch, 1908 was erected for scratched burrows commonly occurring at the base of sandstone beds in the Upper Ordovician Kosov Formation of the Prague Basin, Czechia. The current diagnosis of the ichnogenus *Curvolithus* excludes this ichnospecies, which is now accommodated in the ichnogenus *Tambia* as the new combination *Tambia gregaria* (Fritsch, 1908). *T. gregaria* comprises dominantly crescentic, scratched, sub-horizontal to inclined burrows with a tendency to form clusters. In addition, elongate cylindrical burrows co-occur with *T. gregaria*, but postdate it, and no direct relationship between both traces can be concluded. An arthropod producer (rather than a 'worm') is inferred, but its behaviour remains ambiguous.

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