Trace Fossils of the Werfen Formation

→ Richard Hofmann

Museum für Naturkunde, Berlin, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, 10115 Berlin,
e-mail: richard.hofmann@mfn-berlin.de

ABSTRACT

The Werfen Formation represents an uppermost Changhsingian to lower Triassic shallow marine succession which is exquisitely exposed at the upper reaches of the Bletterbach Canyon and the western slopes of the Weißhorn/Corno Bianco. The macro-invertebrate fauna of these strata is comparatively well known and has been subject to scientific study since the 19th century. Although their presence has been noted early on as well, trace fossils of this formation received almost no attention until the mid-1990's. In this contribution, I give a brief overview of the trace fossils recognised in the Werfen Formation. So far, own investigations have revealed the presence of *Arenicolites* isp., *Asteriacites lumbricalis, Catenichnus contentus, Chondrites* cf. *intricatus* , cf. *Curvolithus* isp., *Didymaulichnus* isp., *Diplocraterion* isp., *Helminthopsis* cf. *abeli, Lockeia siliquaria, Palaeophycus tubularis, Rhizocorallium jenense, Rhizocorallium commune, Planolites montanus, Spongeliomorpha* isp., *Taenidium barretti, Thalassinoides* cf. *suevicus*, and an unidentified arthropod trace. Other authors have additionally reported traces attributable to *Cochlichnus, Dendrotichnium, Skolithos* and a resting trace of an acorn worm. Because the Werfen Formation records ecological conditions after the greatest mass extinction of the Phanerozoic, its ichnofauna has been of particular interest to reconstruct the recovery from this devastating event. Observations from the Griesbachian Mazzin Member suggest that bioturbation virtually vanished during the early post-extinction aftermath with only shallow deposit feeding structures occurring in some levels. A first significant rebound in ichnodiversity and both epi- and infaunal ecosystem complexity is recorded in the lower Seis/Siusi Member with typical subtidal trace fossils such as *Thalassinoides* and *Rhizocorallium* having their first appearance after the mass extinction. The succeeding Gastropod Oolite and Campil Members again record a drop in general bioturbation intensity and trace fossil diversity. Finally, with the presence of comparably larger *Thalassinoides* and *Palaeophycus*-type burrows, the fully marine Val Badia Member signifies the most advanced recovery stages observed in the Werfen Formation.

KEY WORDS

ichnofossils, Triassic, Tethys, extinction, Permian

1. INTRODUCTION

Cropping out in the upper reaches of the Bletterbach Canyon between the Gorz and the slopes of the Weißhorn/Corno Bianco (Fig. 1), the Werfen Formation represents a prominent and, at least its upper part, comparably accessible lithological unit of the local stratigraphic column. It is an approximately 400 metre thick shallow to marginal-marine succession composed of marls, limestones, sandstones and siltstones. Some intervals are abundantly fossiliferous and have attracted the attention of researchers of several generations describing its marine macroinvertebrate fauna (e.g., Wittenburg, 1908; Neri & Posenato, 1985; Twitchett & Wignall, 1996; Nützel, 2005; Posenato, 2008a, 2009; Metcalfe et al., 2011; Hofmann et al., 2015b; Foster et al., 2017), stratigraphy (Bosselini, 1968; Broglio Loriga et al., 1983; Perri, 1991; Perri & Farabegoli, 2003; Posenato, 2008b), palaeoecology and sedimentary environments (Broglio Loriga et al., 1983; Wignall & Hallam, 1992; Twitchett & Wignall, 1996; Wignall & Twitchett, 1996; Nützel & Schulbert, 2005). Since the 1990's, interest in the Werfen Formation increased as these strata provides an insight into the aftermath of the undeniably greatest mass extinction among metazoan biota which occurred towards the end of the Permian (Raup, 1979; Erwin, 1994). Its recovery period became a quite popular research topic across the geoscience-community stimulated by some seminal papers (e.g., Hallam, 1991; Wignall & Hallam, 1992; Schubert & Botttjer, 1995). Trace fossils have been recognised in this unit early on (e.g., Wittenburg, 1908; Leonardi, 1935) and the analysis of ichnological data represented the first serious attempt to gauge the recovery from the end-Permian mass extinction in this palaeogeographic region (Twitchett & Wignall, 1996). However, in contrast to body fossils, trace fossils have never been studied systematically despite they occur throughout the formation in notable abundance to easily catch the attention of laymen and researchers alike. I have been collecting observations on trace fossils in the Werfen Formation rather as scientific garnish to analysing benthic macroinvertebrates (Hofmann et al., 2015b). Based on these efforts I present here an overview on the trace fossils recognised in the Werfen Formation. Observations and samples stem from outcrops dispersed all over the Dolomite region (including the Bletterbach), but it is very likely that similar material can be observed at the western flanks of the Weißhorn/Corno Bianco. Furthermore, I try to highlight the significance of the Werfen Ichnofauna in its evolutionary context.

2. GEOLOGICAL SETTING AND STRATIGRAPHY

The about 400 metre thick Werfen Formation (Fig. 2) is composed of mixed carbonate-siliciclastic rocks (Broglio Loriga et al., 1983) that were deposited on the eastern continental margin of the central Pangaea facing the Tethys ocean (Fig. 3). It is generally interpreted as a shallow marine shelf system ranging from deep subtidal ramp to supratidal, lagoon-like settings. The now widely accepted lithostratigraphical subdivision of

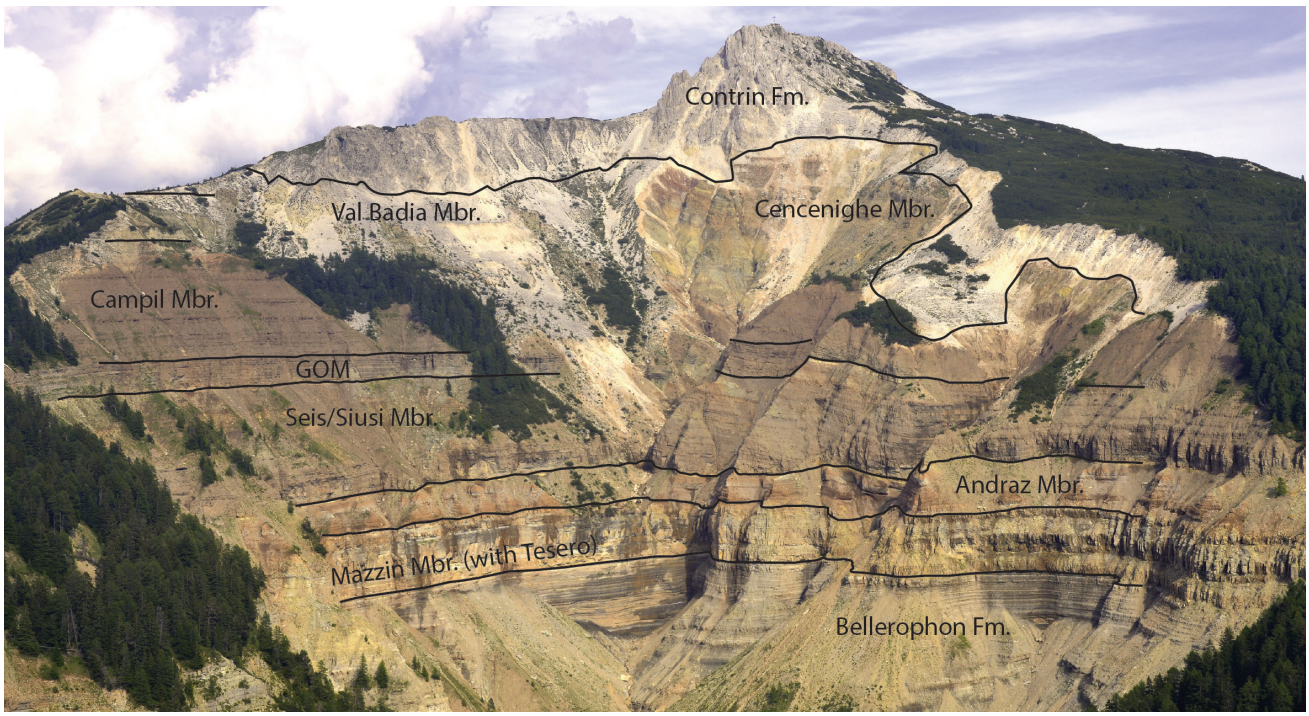

FIG. 1: Aerial view of the western slopes of the Weißhorn/Corno Bianco above the Gorz showing the Werfen Formation and its members (Mbr.). GOM – Gastropod Oolite Member. The zone below the summit of the Weißhorn/Corno Bianco exposes the Val Badia and the Cencenighe mbrs. but is considerably faulted. Therefore supposed boundaries are not marked. Photo courtesy of Peter Daldos/Geoparc Bletterbach.

the Werfen Formation chiefly goes back to Bosselini (1968) and Broglio Loriga et al. (1983) and includes the following units in ascending order: the Tesero Member, the Mazzin Member, the Andraz Member, the Seis/Siusi Member, the Gastropod Oolite Member, the Campil Member, the Val Badia Member, the Cencenighe Member, and the San Lucano Member. The topmost units may be missing due to erosion during the Middle Triassic that locally removed strata down to the upper Seis/Siusi Member. At the Weißhorn/Corno Bianco, youngest Members of the Werfen Formation include the Cencenighe Member and possibly parts of the San Lucano Member which, however, was not observed during field campaigns at this locality. The light-grey rocks that form the summit of the Weißhorn/Corno Bianco pertain probably to the Anisian Contrin Formation. This unit, when preserved, is believed to conformably overlie the Werfen Formation (Broglio Loriga et al., 1983), but is here thrusted upon the older Werfen strata as indicated by the highly irregular (Fig. 1) and tectonised contact between the two.

The Permian-Triassic transition can be observed in an interval stretching from the Bulla Member (the youngest unit of the underlying Bellerophon Formation) across the Tesero Member (also referred to as Tesero Oolite) into the lower part of the Mazzin Member. The main extinction may be observed in the Bulla Member (Posenato, 2008b) or the Tesero Member (Wignall & Hallam, 1992; Noé & Buggisch, 1994; Groves et al., 2007; Farabegoli et al., 2007), respectively. The beginning of the Triassic is defined by the conodont *Hindeodus parvus* whose first appearance has been documented from the Tesero Member (Posenato, 2008b) or the Mazzin Member (Wignall et al., 1996). This local offset in both events is best explained by the highly diachronous facies development during the transgression across the latest Permian interval. The following short descriptions and interpretations of the lithological units are mainly derived from the comprehensive studies of Broglio Loriga et al. (1983, 1990) and own observations (Hofmann et al., 2015). Figure 2 provides an aerial view of the western slopes of the Weißhorn/Corno Bianco with all members.

The Tesero Member is about 6 metre thick but wedges out towards the eastern Dolomites where it is replaced by offshore marls and mudstones. In the Bletterbach, it forms a series of oolitic and bioclastic limestone-beds. These are interpreted oolite-shoals indicating high water energy (i.e. waves and currents) deposited during the early phase of the transgression. The Mazzin Member is between 40 and 50 metres thick and almost entirely composed of laminated marl and mudstone intercalated with some small bioclastic packstone which is typical for subtidal settings below the fairweather wave-base occasionally affect by storm waves. To the top, it becomes shallower and grades into the overlying Andraz Horizon. This unit is up to 25 metre thick and consists of reddish siltstones and yellow dolostones interpreted as supratidal deposits. The succeeding Seis/Siusi Member is about 50 metres thick and in its lower part composed of sandy limestone, packstone, and bioclastic grainstone. These beds are interpreted as a transgressive sequence recording conditions between the upper zone between the fairweather and storm wave-base. This unit grades up-section into more fine-grained deposits recording a distal mid-shelf facies with only rare storm influence. The topmost part of this member is represented by reddish marls and mudstone that are intercalated with thick bioclastic grainstone beds indicating a higher wave-energy level.

The Gastropod Oolite Member is about 20 metres thick and composed of parallel-bedded greyish and reddish calcareous sandstone, marl, and sandy mudstone. A characteristic feature of this unit is the frequent occurrence of purple to pinkish bioclastic grainstones with abundant microgastropods. This unit has a trangsressive base and records the oscillation of water depth between inner and mid-shelf environments, frequently disturbed by high-energy storm events. In the upper part, brownish and

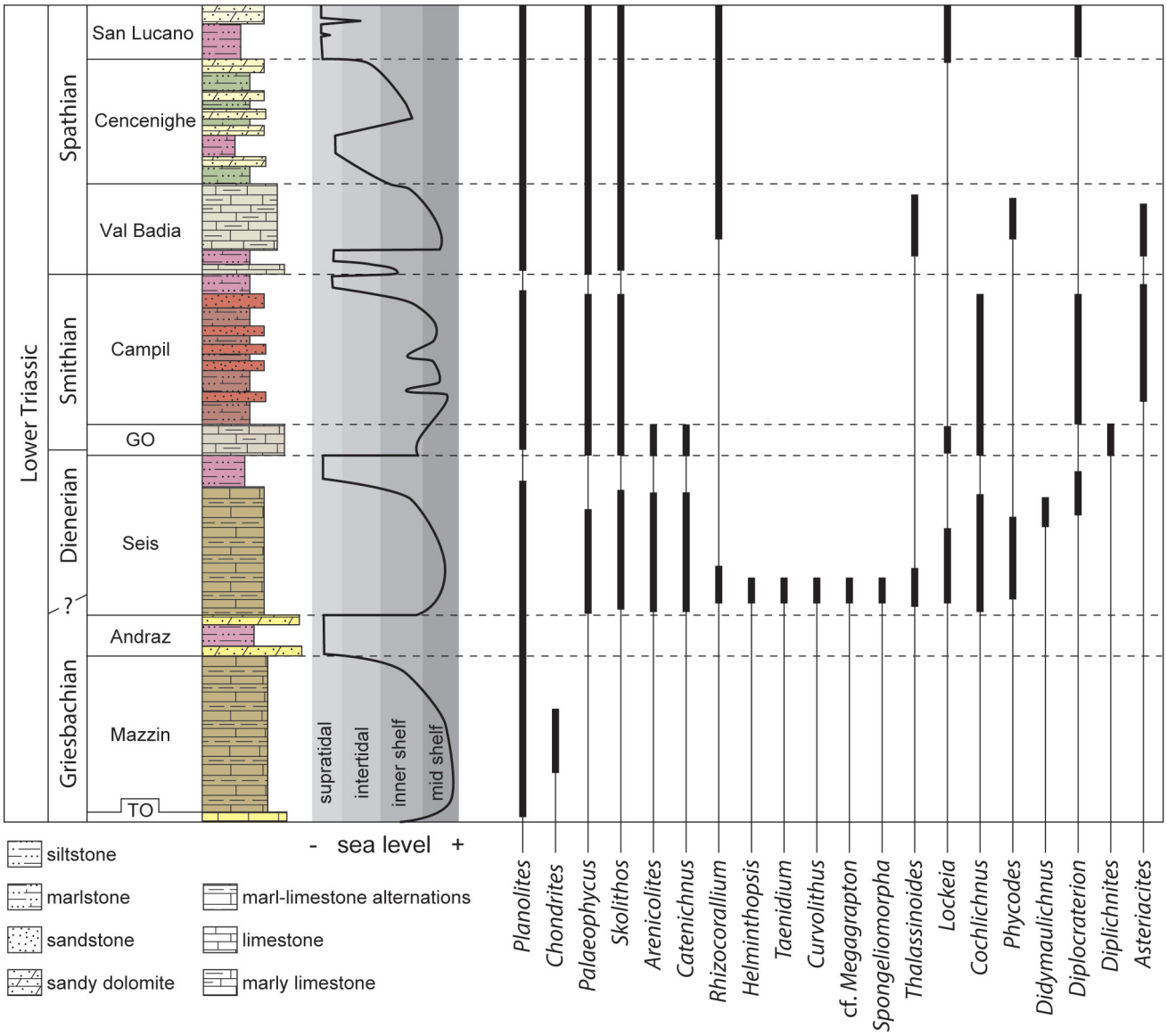

FIG. 2: Idealized stratigraphic section of the Werfen Formation with its members and principal lithology, and reconstructed sea level (after Broglio Loriga et al., 1983) and trace fossil occurrences (after Twitchett & Wignall, 1996; Twitchett & Barras, 2004; Hofmann et al., 2011, observations of this report). The San Lucano Member has not been observed in the Weißhorn/Corno Bianco. At the Weißhorn/Corno Bianco, the whole succession is about 400 metre thick.

reddish siltstone becomes more common. This member grades into the overlying Campil Member. The definite cessation of fully calcareous beds is probably the best "marker" for the base of the Campil beds which are easily recognised as a brown slope-forming unit at the Weißhorn/Corno Bianco. This member attains a thickness of ca. 80 metres and is composed of reddish siltstone and sandstone with very few intercalations of limestone. Most characteristic sedimentary features are thick sheets of sandstone with convolute bedding and ball and pillow-structures, which indicate high sedimentation rates. Also frequently observed are hummocky cross-bedded and ripple-cross laminated sandstones. All these features suggest deposition in a storm- and wave-dominated setting of a mid- and inner shelf setting. Apart from a supratidal siltstone level in the lower third of the unit, the Val Badia Member is composed of marly mudstone, bioclastic grainstone and packstone as well as some calcareous sandstone beds. It is interpreted as a distal mid-shelf succession, which grades upward into shallower, intertidal deposits of the Cencenighe Member. This unit is composed of yellowish calcareous sandstone, pinkish and olive-grey oolithic grainstone as well as reddish and brown siltstone. The fossiliferous calcareous sandstones contain oolites and some reworked shell material indicative of current and wave transport. These beds represent inner and proximal mid-shelf deposits. The calcareous oolite bodies form repetitive, up to 0.5 metres thick sets of tabular and through cross-bedded packages showing alternating flow directions. Reddish siltstones which are sandwiched between these bodies are typically heterolithic. This alternation of facies is interpreted to represent repetitive shallowing-upward cycles starting with shallow subtidal oolite-bars that grade into intertidal mudflats.

3. TRACE FOSSIL CONTENT

The Werfen ichnofauna has never been studied from from an ichnotaxonomic point of view and it is beyond the scope of this contribution to remediate this unfortunate deficiency. Twitchett & Wignall (1996) were the first to report trace fossil

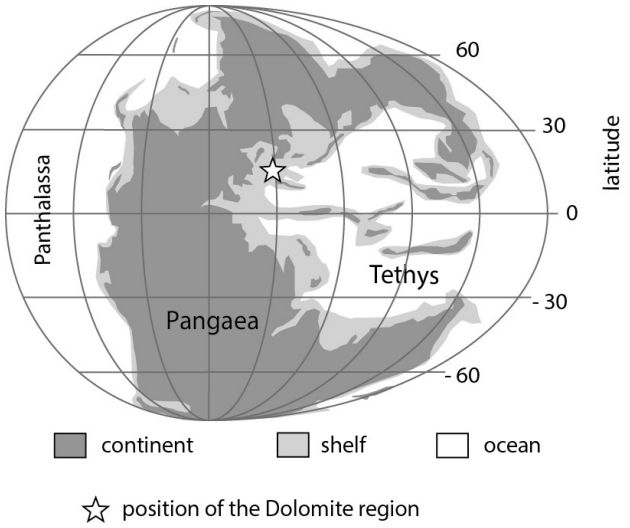

FIG. 3: Palaeogeographic position of the Dolomite region during the Early Triassic. Map after Blakey (2012).

occurrences of the Werfen Formation as a whole. Hofmann et al. (2011) presented observations from the Mazzin Member and for a very narrow interval of the lowermost Seis/Siusi Member. Trace fossils reported in these contributions as well as own unpublished observations are reviewed in the following. The compilation is restricted to figured and identifiable material. As there is no consensus on the classification of trace fossils above the level of ichnogenera, trace fossils are listed alphabetically.

Arenicolites isp. (Fig. 4A): Vertical U-tubes perpendicular to bedding plane preserved as full relief in cross-sectional views. In bedding-plane view *Arenicolites* appears as paired circular openings. The burrows are cylindrical, exhibit a massive, passive fill. Arms typically parallel. Some partially preserved specimens display a J-shaped morphology. *Arenicolites* differs from *Diplocraterion* in the absence of spreiten (Fürsich, 1974a). It is commonly interpreted as a domichnion of suspension-feeding, worm-like organisms (Fürsich, 1974b). However, Bromley (1996) noted that similar structures are produced in modern environments by deposit feeders, including polychaetes, holothurians and enteropneusts.

Asteriacites lumbricalis von Schlotheim, 1820 (Fig. 4B, C): Star-shaped structure with five arms that tapper towards the end. In some cases, the centre of these structures is represented by a circular area. Burrows are typically observed as concave epirelief or, more rarely, as convex hyporelief. Fine striae may be preserved within arms. Morphology, taxonomy, and ecological significance of *Asteriacites* were thoroughly reviewed by Mángano et al. (1999) and the material of the Werfen Formation is best placed within the most common ichnospecies *A. lumbricalis*. These trace fossils are easily identified as resting and possibly feeding traces of asterozoans such as star fish and brittle stars. The ichnogenus ranges in age from the Cambrian to the recent (Mikuláš, 1992a) and is most commonly observed in shallow subtidal and restricted marine deposits (Mikuláš, 1992; Mángano et al., 1999). *Asteriacites* is one of the earliest known trace fossils reported from the Werfen Formation (e.g., Wittenburg, 1908) and is particularly abundant in the Campil Member. The fine-scale intercalation of sand- and siltstones as well as the absence of profound biogenic sediment mixing in this unit provide excellent preservation potential (see discussion for further details). It has also been reported from the upper Seis/Siusi- and the Val Badia Member (Twitchett & Wignall, 1996).

Catenichnus contentus McCarthy, 1979 (Fig. 4E): Vertical, cylindrical U-shaped burrow. It typically shows retrusive spreiten which indicate a stepwise downward movement of the tube (the "old" upward-facing burrow-wall then becomes one laminae of the spreite-structure). Arms are not parallel and highly diverging. *Catenichnus* differs from similar ichnogenera *Diplocraterion* and *Arenicolites* in lacking parallel arms. *C. contentus* is the only ichnospecies of *Catenichnus* and the material from the Werfen Formation corresponds readily with its diagnosis (McCarthy, 1979). *Catenichnus* is interpreted as a dwelling burrow of suspension feeders (McCarthy, 1979). This ichnogenus ranges in age from late Cambrian (Fillion & Pickerill, 1990) to the Early Triassic (Twitchett & Wignall, 1996) and appears to be restricted to moderate and high energy shallow marine environments (Fillion & Pickerill, 1990; McCarthy, 1979). In the Werfen Formation, it appears to be restricted to the lower Siusi Member (Twitchett & Wignall, 1996; own observations)

Chondrites cf. *intricatus* (Brongniart, 1823) (Fig. 4D): Small burrows which show mostly a bifurcate branching pattern. Preserved as full relief structures with burrow-filling being darker than the host rock. *Chondrites* generally forms tree-shaped tunnels with a more or less regular branching pattern. Branching occurs from one main tunnel that protrudes into the sediment. The specimens observed in the Werfen Formation are highly compacted which somewhat obliterates the root-like appearance of these traces. However, true branching is unequivocally present which distinguishes this trace from superficially similar *Planolites* (see below). If seen in cross-sectional view, the protruding nature of *Chondrites* becomes also apparent. A thorough review of this Ichnogenus was carried out by Fu (1991) who recognised few of the available ichnospecies as valid; *C. targonii*, *C. intricatus*, *C. patulus*, and *C. recurvus* [but see Uchman (1999) for further ichnospecies and update of the taxonomic concept of *Chondrites*]. The material from the Werfen Formation may be best placed in *C. intricatus*, which is characterised by small tunnels, and radial, downward-facing acute bifurcations. Because the radial branching pattern is not observed in the material presented herein, an open nomenclature is preferred. *Chondrites* is most likely a structure of chemosymbionts (Fu, 1991) with a number of proposed producers including polychaetes, sipunculids, arthropods, and bivalves (Fu, 1991; Uchman, 1999; and references therein). Chemosymbiotic bivalves of the genus *Thyasira* are unequivocally associated to *Chondrites*-type burrows in recent marine environments (Seilacher, 1990). Oldest representatives of *Chondrites* are Cambrian in age (Crimes, 1987).

cf. *Curvolithus* isp. (Fig. 4F): This ichnogenus comprises flat, ribbon-like, interstratal structures, which show a characteristic multilobate morphology (Buatois et al., 1998a). The specimen observed in the Werfen Formation is poorly preserved and identification tentative (Hofmann et al., 2011). Alternatively, it represents a burrow which might interpreted as *Spongeliomorpha* although it lacks branching and a clear ornamentation. *Curvolithus* is believed to have been produced by infaunal carnivores, possibly gastropods, flatworms, or nemerteans (Buatois et al., 1998a). It is reported from various marine environments but

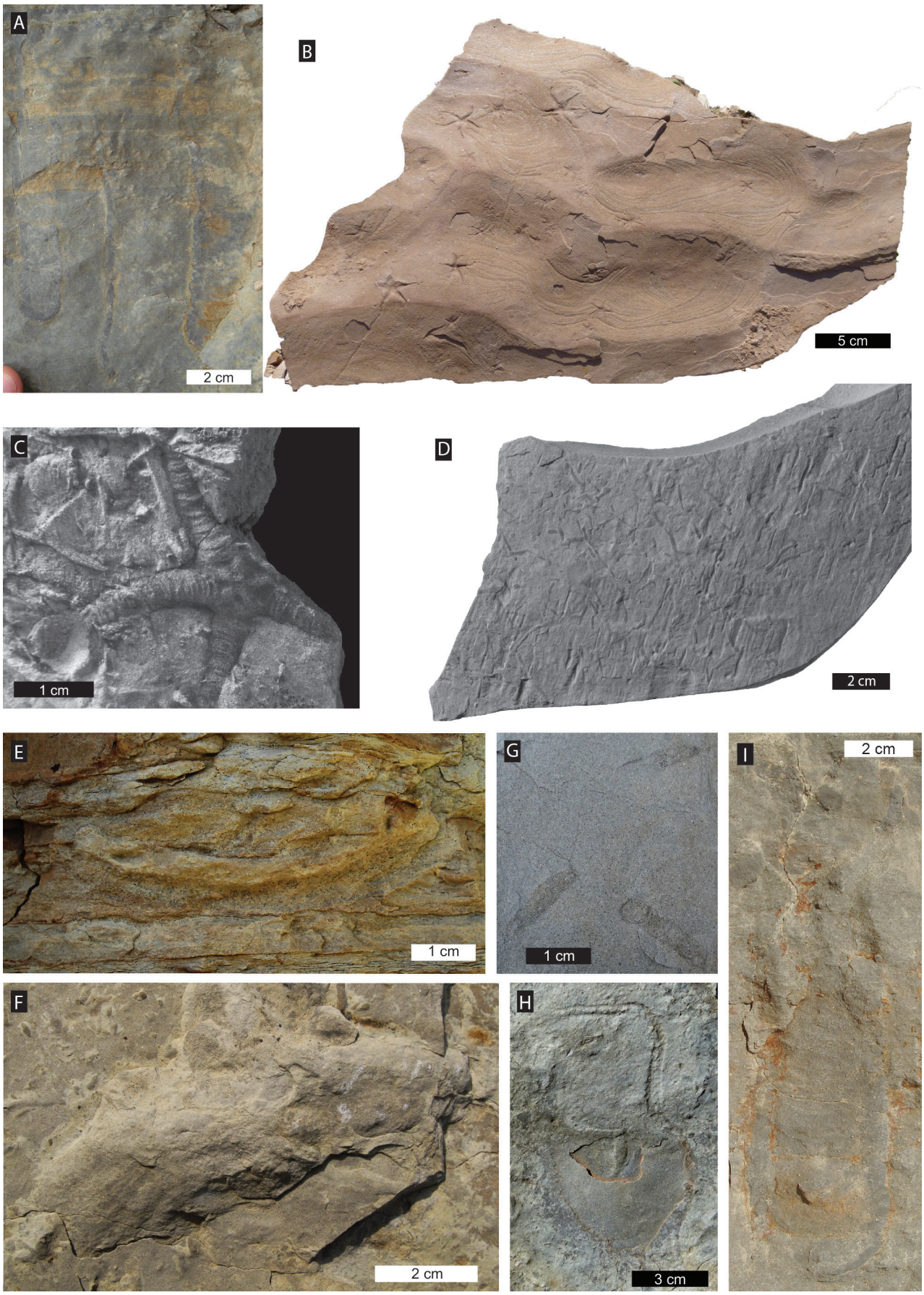

FIG. 4: Trace fossils of the Werfen Formation. **(A)** *Arenicolites* isp., Val Badia Member, Costabella. (**B**) *Asteriacites lumbricalis*, Campil Member, Weißhorn. (**C**) *Asteriacites lumbricalis*, Campil Member, Rosengarten/Catinaccio. (**D**) *Chondrites* cf. *intricatus*, Mazzin Member, Aferer Geisler. (**E**) *Catenichnus contentus*, lower Seis/Siusi Member, Rosengarten/Catinaccio. (**F**) cf. *Curvolithus* isp., Seis/Siusi Member, Rosengarten/Catinaccio. (**G**) *Diplocraterion* isp. upper Seis/Siusi Member, Aferer Geisler. (**H**) *Didymaulichnus* isp., upper Seis/Siusi Member, Rosengarten/Catinaccio. (**I**) *Diplocraterion* isp. Val Badia Member, Costabella.

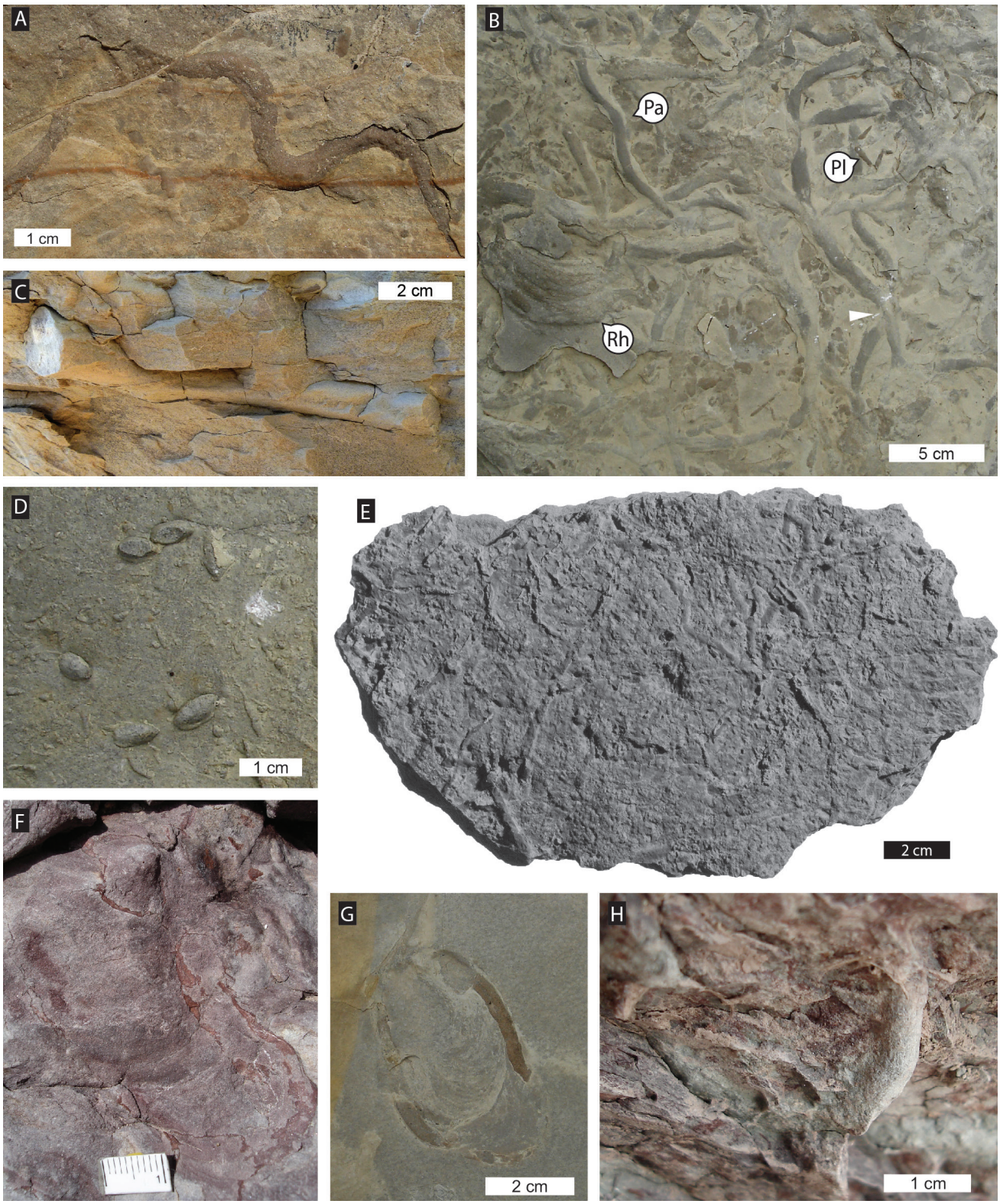

FIG. 5: Trace fossils of the Werfen Formation. (**A**) *Helminthopsis* cf. *abeli*, lower Seis/Siusi Member, Rosengarten/Catinaccio. (**B**) *Palaeophycus tubularis* (Pa), *Planolites montanus* (Pl), and spreiten-structures attributable to *Rhizocorallium* (Rh), lower Seis/Siusi Member, Rosengarten/Catinaccio. (**C**) *Palaeophycus tubularis,* Val Badia Member, Weißhorn/Corno Bianco. (**D**) *Lockeia siliquaria*, Seis/Siusi Member, Col Rodella. (**E**) *Planolites montanus*, Mazzin Member, Aferer Geisler. (**F**) *Rhizocorallium jenense*, San Lucano Member, Val Venegia. (**G**) *Rhizocorallium commune*, lower Seis/Siusi Member, Rosengarten/Catinaccio. (**H**) *Rhizocorallium jenense,* San Lucano Member, Val Venegia.

seems to be a characteristic element of subtidal settings (Buatois et al., 1998a). It ranges in age from late the Precambrian (Webby, 1970) to the Miocene (Keij, 1965). In the Werfen Formation *Curvolithus* has only been observed in the lower Seis/Siusi-Member.

Didymaulichnus isp. (Fig. 4H): Irregular trails consisting of two smooth furrows separated by median ridge (bilobate structure). The structure is preserved as concave hyporelief. *Didymaulichnus* is very similar to small representatives of the ichnogenus *Cruziana* (*Cr. problematica*) but differs in the absence of any or-

namentation within the furrows. *Didymaulichnus* is interpreted as surface trail of gastropods (Vossler et al., 1989) but euthycarcinoid body fossils unequivocally associated to such traces (Collette et al., 2010) render arthropods as likely producers. Crimes (1975) suggested trilobites as producers of *Didymaulichnus*. It ranges in age from the earliest Cambrian or terminal Precambrian (Jensen et al., 2006) to the later Cretaceous (Vossler et al., 1989). It seems to be especially common in the lower Palaeozoic (Collette et al., 2010; Pickerill et al., 1984b). *Didymaulichnus* is typically observed in marginal marine successions (Collette et al., 2010; Vossler et al., 1989). This is the first report of this trace fossil in the Werfen Formation.

Diplocraterion isp. (Fig. 4G, I): Vertical U-tube burrows perpendicular to bedding plane preserved in full relief in cross sectional views. Spreiten-structures occur between the arms. On bedding-planes, *Diplocraterion* is expressed as paired circular opening with contorted zone inbetween that superficially resemble dumb-bells. *Diplocraterion* is interpreted as a burrow of suspension feeders (Seilacher, 1967; Cornish, 1986; Fürsich, 1974b). The spreite in *Diplocraterion* most probably reflect animal growth or adjustment to sedimentation and erosional processes (equilibrichnia of Bromley, 1996). Thus, it can be interpreted as a dwelling tube or an equilibrium structure of a suspension-feeding organism. Bromley (1996), however, noted that *Diplocraterion*-like structures in recent muddy substrates are produced by detritus-feeding amphipods. *Diplocraterion* ranges in age from the Cambrian to the Holocene.

Helminthopsis cf. *abeli* Książkiewicz, 1977 (Fig. 5A): Horizontal subcylindrical burrow with an irregularly meandering course. The material observed in the Werfen Formation might be best placed in *H. abeli* which is characterised by irregular, open meanders and horseshoe-like turns in Wetzel & Bromley (1996) who gave a thorough systematic revision of the ichnogenus. However, horseshoe-like turns are not readily observed the structure observed by Hofmann et al. (2011) so it was identified in open nomenclature. *Helminthopsis* is interpreted as deposit feeding structure (Buatois et al., 1998b) of polychaetes and probably priapulids (Fillion & Pickerill, 1990), at least for marine occurrences (but see Buatois et al., 1998b). It ranges in age from late Precambrian (Gibson, 1989) to Holocene (Swinbanks & Murray, 1981). *Helminthopsis* is usually recorded in deep marine settings (Książkiewicz, 1977) but it occurs in various subaqueous environments, too (Buatois et al., 1998b).

Lockeia siliquaria James, 1879 (Fig. 5D): Almond-shaped traces preserved as convex hyporelief. The most widely reported ichnospecies of *Lockeia* is *L. siliquaria*, which comprises smooth, almond shaped structures which typically show a tapered and a more rounded end (Mángano et al., 2002). This is observed in a couple of specimens. *Lockeia* is a resting trace typically produced by bivalves (Seilacher, 1953). This ichnogenus ranges in age from upper Cambrian/lower Ordovician (Fillion & Pickerill, 1990) to the Pleistocene (Pemberton & Jones, 1988). *Lockeia* is a facies crossing form and present in all marine and fresh water environments (Mángano et al., 2002). It is an abundant ichnotaxon in the Werfen Formation and most commonly observed in the Seis/Siusi-Member, the Gastropod Oolite-Member, as well as the Val Badia Member.

Palaeophycus tubularis Hall, 1847 (Fig. 5B, C): Straight to irregularly sinusoidal, horizontal, thinly lined cylindrical burrows, preserved as epirelief and hyporelief, in both positive and negative. Surface is generally smooth. Fill is massive and mostly identical to host rock. False branching as a result of overlapping specimens may occur. Pemberton & Frey (1982) provided an extensive review on this kind of traces (i.e. simple, horizontal, unbranched tubes) and generally recommended to place actively filled burrows in *Planolites* and passively filled burrows to *Palaeophycus*. Passive fill means that open burrows were filled with ambient sediment by physical process. Active fill implies that the burrow was filled with digestive products or ambient sediment that was stuffed into the burrow by its producer. *Palaeophycus tubularis* is distinguished from other ichnospecies of *Palaeophycus* by a thin lining and the absence of striations. *Palaeophycus* most likely represents a dwelling burrow of suspension-feeding or predatory worms (Pemberton & Frey, 1982). This ichnogenus is common in practically all terrestrial and sub-aquatic environments (Pemberton & Frey, 1982), and ranges in age from Ediacaran (e.g., Seilacher et al., 2005) to Holocene (e.g., Gingras et al., 2008).

Planolites montanus Richter, 1937 (Fig. 5B, E): Indistinct, sub-cylindrical to cylindrical, horizontal burrows with smooth surface mostly preserved as full-reliefs. Burrow fill darker than host rock. *Planolites montanus* is distinguished from other ichnospecies of *Planolites* by its small size, tortuous course, penetrative nature and lack of ornamentation (Pemberton & Frey, 1982). This structure is interpreted as deposit feeding burrow of infaunal vermiform organisms (Pemberton & Frey, 1982). *Planolites* is a facies-crossing ichnotaxon which has been documented from all marine and continental environments (Pemberton & Frey, 1982). It ranges in age from the uppermost Neoproterozoic (e.g., Narbonne & Hofmann, 1987) to the Pleistocene (e.g., Pemberton & Jones, 1988). *Planolites montanus* can be observed in virtually all parts of the Werfen Formation. However, it is especially common in the Mazzin Member, where it is the only discernible trace fossil.

Rhizocorallium jenense Zenker, 1836 and *Rhizocorallium commune* Schmid, 1876 (Fig. 5F, G, H, 6F): Oblique to horizontal U-shaped burrow with spreiten-structures between the arms.

Knaust (2013) gave a comprehensive overview on this ichnogenus discussing its relationship to similar ichnogenera, possible producers, valid ichnospecies, and environmental significance. *Rhizocorallium* is, in contrast to other U-shaped burrows (*Arenicolites*, *Diplocraterion*), characterised by its horizontal or oblique orientation.

This ichnogenus is interpreted as a suspension and deposit feeding burrow, most likely of crustaceans, polychaetes, and insects (Fürsich, 1974b; Knaust, 2013). *Rhizocorallium* is typically observed in shallow marine deposits (Fürsich, 1974b) but occurs in various settings including deep marine (Uchman, 1991), marginal marine (Hakes, 1976) and non-marine (Fürsich & Mayr, 1981). It ranges in age from Cambrian (Seilacher, 1955) to Miocence (Fürsich & Mayr, 1981). The two currently accepted ichnospecies of *Rhizocorallium* are *R. jenense* and *R. commune* (Knaust, 2013). *R. jenense* typically represents obliquely inclined subsurface burrows with closely spaced net-like scratches that are indicative of firmground-conditions. Although obliquely entering the sediment column as well, *R. commune* tends to form horizontal burrows within the sediment, and it characteristically contains fecal pellets in its spreiten (Knaust, 2013).

Both forms can be recognised in the Werfen Formation. Short, oblique U-shaped burrows (*R. jenense*) are very common in the inter- to supratidal portions of the Cencenighe- and San Lucano Members (Twitchett & Wignall, 1996; own observations). *R. commune* is observed in fully marine portions of the Seis/Siusi- and the Val Badia Members.

Spongeliomorpha isp. (Fig. 6A): Subcylindrical, horizontal burrow with irregular longitudinal striae. The preserved burrow is more than 20 cm long and follows an irregular course. It displays short branching segments, which diverge almost perpendicular from the main structure. Branches are straight and 2 mm to 4 mm wide. One branching segment is tear-shaped showing an increasing diameter towards its terminal end. Because of its similar general morphology and the tendency to show intergradational stages, *Thalassinoides, Ophiomorpha* and *Spongeliomorpha* have been suggested to be synonymous (Fürsich, 1973b), which did not find generally agreement among ichnologists (Bromley & Frey, 1974). This is mainly because the distinctive characteristics of the burrow wall (smooth vs. striated vs. pelletal lining) in fact reflect behavioural differences that justify a separation on the ichnogeneric level. *Spongeliomorpha* represents a deposit feeding and dwelling burrow of produced by crustaceans (Bromley, 1967) and is most common in shallow marine environments (Schlirf, 2000).

Taenidium barretti (Bradshaw, 1981) (Fig. 6E): Horizonal burrow with meniscate backfill. Burrow course is highly irregular and secondary branching occurs. The most accepted revision of meniscate backfilled burrows is that of Keighley & Pickerill (1994) who assigned the trace fossil originally erected as *Beaconites barretti* (Bradshaw, 1981) to *Taenidium*. The specimen from the Seis/Siusi Mb. readily corresponds with the diagnosis provided by Keighley & Pickerill (1994) and the slightly emended diagnosis of Schlirf (2000). *Taenidium* is interpreted as deposit feeding structure (Squires & Advocate, 1984) of worm-like animals (Schlirf, 2000). It is a facies crossing form (see Keighley & Pickerill (1994) and references therein) but *T. barretti* appears to be more common in terrestrial environments (Keighley and Pickerill, 1994). The ichnogenus ranges in age from Silurian (Dam & Andreasen, 1990) to the Pleistocene (D'Alessandro et al., 1992).

Thalassinoides cf. *suevicus* (Rieth, 1932) (Fig. 6B, C, D): Description: Horizontal, subcylindrical systems of irregular, smooth burrows with mostly dichotomous, Y-shaped branchings. Swellings at the sites of branching is frequently observed. These burrows are preserved as full relief structures. The problems in demarcating *Spongeliomorpha* and *Thalassinoides* are presented in the discussion on *Spongeliomorpha*. The specimens from the Werfen Formation are composed of horizontal burrow systems with dichotomous bifurcations that show a slight increase in the diameter. Thus, they largely correspond with the diagnosis of *Thalassinoides suevicus* [*Spongeliomorpha suevicus* in Fürsich (1973a) and Schlirf, (2000)]. *Thalassinoides* is widely accepted to represent a deposit feeding and dwelling burrow of crustaceans (Fürsich, 1973c) and it is reported from deep marine (Uchman, 1995) and, more commonly, shallow marine environments (Fürsich, 1973a; Schlirf, 2000). The presumably oldest *Thalassinoides*-traces are reported from the Cambrian (Sprechmann et al., 2004). Modern burrows produced by a multitude of crustaceans correspond with the morphology of *Thalassinoides*-trace fossils.

Unidentified ?arthropod trace (Fig. 6G): This structure is 6 cm wide and of unknown length (11 cm preserved on a slab). It can chiefly been described as a number of irregular scratch-like contortions that are preserved as convex hyporelief. It is somewhat suggestive to be composed of two rows of scratches. Such a structure may be assignable to *Diplichnites* Dawson, 1873 – an arthropod walking trace – but the material is just too irregular to be confidently placed within this genus. In the upper third of the structure, there appears to be a small ridge (black arrow in figure 6G, a furrow in the original substrate) which resembles a telson drag-mark. Some "scratches" (white arrows in Figure 6G) may be of abiotic origin as they are very similar to synaeresis cracks – a sedimentary structure indicative of substrate shrinkage induced by salinity fluctuations. This casts some doubt of this "trace" to be of biologic origin altogether. If biogenic, it is likely attributable to the activity of arthropods because such rather delicate scratches are most notably reflect substrate modification by hard appendages. This structure was observed in the Campil Member.

4. ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE

The Werfen ichnofauna gains its importance from the evolutionary-ecological context. The Werfen Formation represents one of the most continuous succession of strata spanning the aftermath of the end-Permian mass extinction and thus offers insight into an important episode in the history of life. As trace fossils usually capture *in situ* signals on the ecology they have been acknowledged as important tool to reconstruct the restoration from this devastating event (Wignall & Hallam, 1992; Twitchett & Wignall, 1996; Pruss & Bottjer, 2004; Beatty et al., 2008; Hofmann et al., 2011).

First of all, the Mazzin Member impressively shows the near-complete cessation of bioturbation either as a result of persistent environmental stress (Wignall & Twitchett, 1996) or the extinction of bioturbators (Erwin, 1993; Hofmann et al., 2011). Deposits of this facies (shallow subtidal) are usually heavily bioturbated and host, if preserved, a number of ichnotaxa organised in complex ichnoassemblages (Buatois & Mángano, 2011). However, trace fossils in this unit are restricted to simple burrows such as *Planolites* and small specimens of *Chondrites*. Both burrows may be indicative of stressed, typically oxygen-restricted, conditions (Savrda & Bottjer, 1986).

The picture changes during the next transgression above the Andraz Member, when subtidal deposition resumed on the Werfen Shelf. The lower beds of the Seis/Siusi Member host a fairly diverse ichnofauna including a number of ichnotaxa that are indicative of normal marine conditions. Most notable examples are the crustacean dwelling burrows *Thalassinoides* or *Spongeliomorpha* as well as dwelling and feeding-structures like *Rhizocorallium*. Infaunal activity of possible carnivores is indicated by *Palaeophycus* and *Curvolithus*. Burrows of infaunal suspension feeders include *Diplocraterion* and *Catenichnus*. The upper part of the Seis/Siusi Member records marginal marine (i.e. intertidal and supratidal) conditions with only sparse infaunal activity. Only some ripple-cross laminated sand- and siltstones occasionally contain *Diplocraterion* and *Lockeia*. Own Field observations in the Gastropod Oolite Member suggest that bioturbation is mostly restricted to very shallow bivalve-resting traces *Lockeia* and *Planolites*. In addition, *Diplocraterion*, *Skolithos* and an acorn worm resting trace (Twitchett, 1996) were reported to occur in this

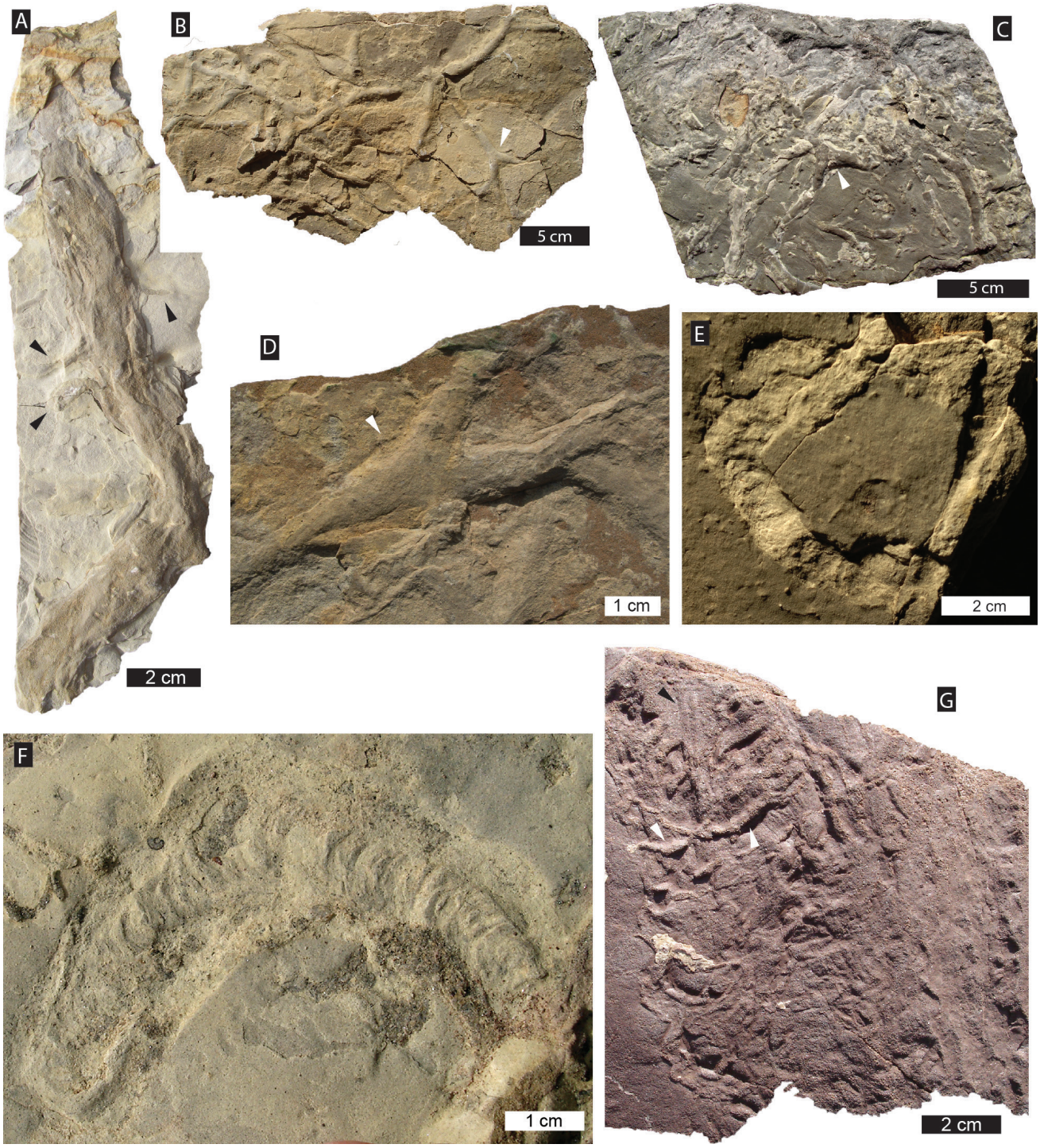

FIG. 6: Trace fossils of the Werfen Formation. (**A**) *Spongeliomorpha* isp., black arrows point to small branching structures, lower Seis/Suisi Member. (**B**) Slab with *Thalassinoides* cf. *suevicus* showing characteristic bifurcuations. (white arrow), lower Seis/Siusi Member, Rosengarten/Catinaccio. (**C**) *Thalassinoides* cf. *suevicus*, white arrow pointing to swelling at the sites of branching which is typical for *Th. suevicus*, Seis/Siusi Member, Aferer Geisler. (**D**) *Thalassinoides* cf. *suevicus* showing characteristic bifurcation and swelling (white arrow), lower Seis/Siusi Member, Rosengarten/ Catinaccio. (**E**) *Taenidium barrette*, lower Seis/Siusi Member, Rosengarten/Catinaccio. (**F**) *Rhizocorallium commune*, upper Seis/Siusi Member, Aferer Geisler. (**G**) Unidentified arthropod-trace, Campil Member, Costabella. White arrows point to proable syneresis cracks. Black arrow points to questionable telson drag-mark.

Member. However, bioturbation is still generally scarce. This is inasmuch remarkable given that the Gastropod Oolite unit is interpreted to record a similar facies range in which the relatively complex trace fossil assemblages of the lower Seis/Suisi Member are observed. It has been suggested (Hofmann et al., 2011, 2015b; Pietsch et al., 2016, Foster et al., 2017) that benthic ecosystems suffered from a second episode of environmental stress across the Dienerian-Smithian transition, which would explain the low diversity and paucity of bioturbation in this unit.

The Campil Member again records the facies range between the fair-weather and the storm-wave base which is typically characterised by high bioturbation rates and a notable diversity of trace fossils (MacEachern & Pemberton, 1992). However, strata of the Campil Member appear eerily underbioturbated. Only the shallow ophiuroid (brittle stars) resting trace *Asteriacites*, for which this member is well known, occurs in notable abundances. Very rarely observed is *Diplocraterion* (Twitchett & Wignall, 1996). This lack in bioturbation is most easily

explained by three things. First, the Campil Member records a pronounced episode of continental runoff on the Werfen Shelf which almost certainly imposed significant stress factors (i.e. high sedimentation rates, turbid waters, salinity fluctuations) on the shallow-marine fauna. Second, reduced preservation potential due to high sedimentation rates. Third, probable absence of major marine bioturbators as a result of the second extinction presumably at the end of the Dienerian or early Smithian (Hofmann et al., 2015b). Additionally, geochemical data have shown that the Smithian time interval, during which the Campil Member was deposited, records harsh temperature changes (Sun et al., 2012; Romano et al., 2013) that culminated in the most profound marine extinction within the Early Triassic (Galfetti et al., 2007). However, stratigraphic control in the Campil Member is virtually absent and might be the case that these critical intervals are not recorded in these sections. Other Phanerozoic deposits of similar facies holding the same environmental challenges to the benthos may be characterised by profound bioturbation (e.g., MacEachern & Pemberton, 1994; Buatois et al., 2008). It is therefore likely that scarce bioturbation in these beds in fact reflects interregional environmental stress and/or long-term effects of the extinction. No bioturbation has been observed in the supratidal horizons of the upper Campil and lower Val Badia Member.

Fully marine deposits of the Val Badia Member signify the establishment of a rather "normal" ichnofauna. Typically observed are *Palaeophycus*, *Planolites*, *Diplocraterion*, and *Thalassinoides.* Twitchett & Wignall (1996) report *Asteriacites* and *Skolithos* in this unit. In the more calcareous lithologies of this member, trace fossils are usually not very well preserved as diagenetic processes in carbonates tend to eradicate biogenic structures (Pickerill et al., 1984a). Furthermore, general rates of bioturbation seem to increase in this member, which significantly lowers the preservation potential of shallow traces (Buatois & Mángano, 2013). Both aspects combined somewhat hinder to acknowledge the full ichnodiversity of this unit. Previous studies (Twitchett & Wignall, 1996) as well as palaeoecological analyses of body fossils (Hofmann et al., 2015a) have shown that the Val Badia Member indicates most advanced recovery stages in the Werfen Formation.

The shallow intertidal to supratidal deposits of the overlying Cencenighe Member document a decline in ichnodiversity (Fig. 2; Twitchett & Wignall, 1996; Twitchett & Barras, 2004). This most likely reflects stressed environmental conditions in such habitats including high temperatures, fluctuating salinities as well as transient subaerial exposure. In the San Lucano Member, rather complex suites containing *Diplocraterion* and *Rhizocorallium* show that these stressed environments became populated by the end of the Early Triassic in that region.

5. CONCLUDING REMARKS

Although the Werfen ichnofauna still holds a promising prospect for further exploration, so far recognised ichnotaxa provide robust insight into the ecological restoration from the end-Permian mass extinction. Especially the comparison of subtidal deposits of the key intervals (Griesbachian: Mazzin Member; Dienerian: Seis/Siusi Member; Smithian: Campil Member; Spathian: Val Badia Member) shows that recovery progressed towards the Early/Mid-Dienerian but was significantly reset during the Smithian time interval. Whether this recession is caused by local environmental stress (high input of siliciclastic material) or global perturbations (drastic temperature changes) cannot be conclusively answered by looking at the Werfen Ichnofauna alone. The (re)establishment of ichnotaxa typically observed in post-Palaeozoic subtidal environments in the Spathian occurred relatively swift and probably presented the root of the Mesozoic ecosystems staffed by the definite survivors of the end-Permian and the, still poorly understood, intra-Early Triassic mass extinctions.

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