FIRST REPORT ON SWIMMING TRACE FOSSILS OF FISH FROM THE UPPER PERMIAN AND LOWER TRIASSIC OF THE DOLOMITES (ITALY)

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Abstract: In the Upper Permian continental to marginal-marine succession of the Southern Alps (Dolomites, north Italy), the ichnological record consists of diverse vertebrate footprints and non-diverse invertebrate trace fossils, mainly occurring in the "Bletterbach ichnoassociation" of the Val Gardena Sandstone Formation. After the Permian-Triassic Boundary event, vertebrate ichnoassociations are scarce until the Middle Triassic (Anisian), whereas the uppermost Permian–Lower Triassic Werfen Formation preserves a rich invertebrate trace-fossil record. To date, fish body and trace fossils (*Undichna*) are very rare in the pre- and post-extinction deposits of the Dolomites; only *Undichna gosiutensis* Gibert, 2001 was identified in the "Voltago Conglomerate" (Middle Anisian), whereas some unidentified fossil fish casts were found in the Permian Val Gardena Sandstone and some fish remains in the overlying Werfen Formation.

Recently, for the first time, fish trails have been discovered in the Val Gardena Sandstone (Lopingian) and in the Werfen Formation (Campil member, Early Triassic, Smithian). Val Gardena Sandstone yielded *Undichna* cf. *quina* Trewin, 2000 and *U. bina* Anderson, 1976 and these represent the oldest fish trails found in the Southern Alps so far. Conversely, the specimens found in the Werfen Formation can be assigned to *Undichna* cf. *britannica* Higgs, 1988. They represent the oldest Mesozoic record of fish trace fossils in northern Italy and one of the few records of *Undichna* from marine environments. These trace fossils are consistent with the fossil association found in the two formations and reflect fish swimming activity in different environments: in very shallow, calm, brackish distal-floodplain to marginal-marine environments in the Late Permian, in association with abundant and diverse tetrapod tracks, and non-diverse invertebrate trace fossils, and in inter- to subtidal calm, shallow, marine environments in the Early Triassic, together with abundant, but not diverse invertebrate trace fossils.
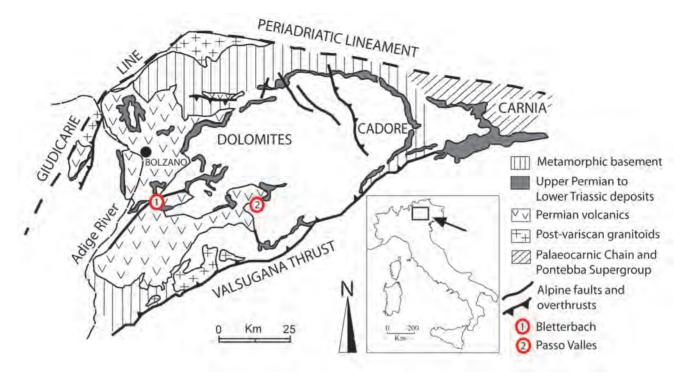
Key words: Trace fossils, *Undichna*, Permian, Triassic, northern Italy.

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INTRODUCTION

Trace fossils, being rarely transported, represent an *in situ* record of ancient biogenic activities, and in shallow marine settings, can provide an important insight into benthic life (e.g., Seilacher, 1967; Leonardi, 1987; Buatois and Mángano 2011). This work deals with the recent discovery of *Undichna* fish trails in the Upper Permian and Lower Triassic deposits of the Southern Alps of Italy (Fig. 1). They

represent the first record of fish trace fossils in the stratigraphical units below and above the Permian-Triassic Boundary (PTB). Undetermined fish casts are known from Upper Permian strata (Conti *et al.*, 1975) and other fossil remains, referred to *Archaeolepidotus leonardi* and *Paralepidotus? moroderi*, were determined by Accordi (1955, 1956). According to this author, they were found in the Lower

Fig. 1. Simplified geological map of the Dolomites, Italy (redrawn from Massari *et al.*, 1994). Red circles mark the *Undichna* study sites. Inset shows the relative position of the study area within Italy.
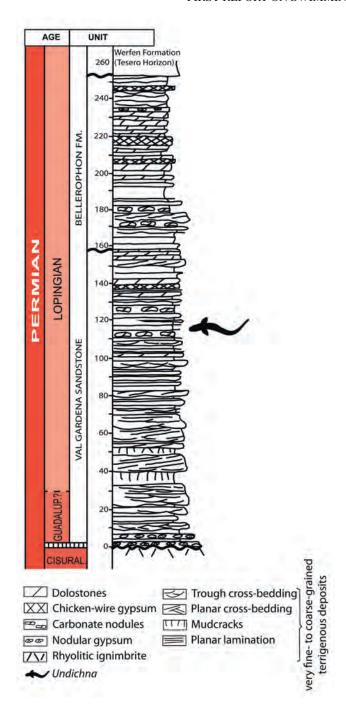
Triassic Werfen Formation, but they probably should be referred to the Permian Bellerophon Formation (Sirna *et al.,* 1994; Blieck *et al.*, 1997).

Rich ichnoassociations, including vertebrate footprints (Avanzini *et al.*, 2011; Marchetti *et al.*, 2017c and references therein) and the traces and trackways of invertebrates (Conti *et al.,* 1977; Twitchett and Wignall, 1996; Hofmann *et al.*, 2011; Baucon and Neto de Carvalho, 2016), have been widely reported from the Upper Permian (Lopingian) – Triassic continental successions of the Dolomites.

Starting from the diagnoses and classification of Anderson (1970, 1976) and Fliri *et al.* (1970), trails of fish origin (*Undichna*) have been identified in different areas in strata dating back to the Devonian (Morrissey *et al.*, 2004; Wisshak *et al.*, 2004). After some pioneering works (Higgs, 1988; Turek, 1989), comprehensive revisions and descriptions of new ichnospecies have been proposed (Buatois and Mángano, 1994; Gibert *et al.*, 1999; Trewin, 2000; Gibert, 2001; Soler-Gijón and Moratalla, 2001; Morrissey *et al.*, 2004; Minter and Braddy, 2006; Costeur and Ezquerra, 2009; Buatois *et al.*, 2010; Bordy *et al.*, 2011; Lu *et al.*, 2012). To date, in the Southern Alps, records of *Undichna* have been reported only by Todesco and Avanzini (2008), who identified *Undichna gosiutensis* Gibert, 2001 in the "Voltago Conglomerate" (Anisian, Middle Triassic). The new fish trails were discovered in the Val Gardena Sandstone (Late Permian) and in the Campil member of the Werfen Formation (Early Triassic, Smithian) and shed new light on the fauna that lived in the Southern Alps during the Permian-Triassic transition.
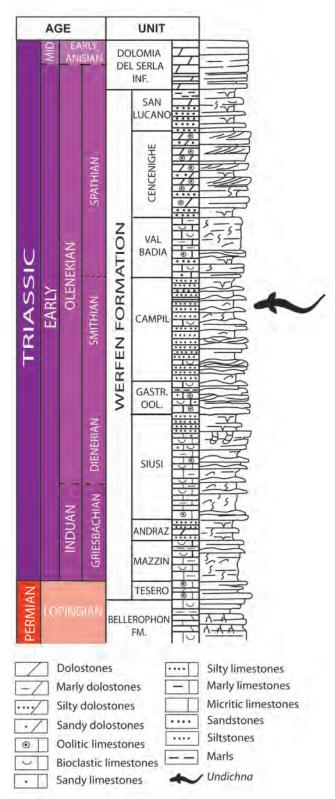
GEOLOGICAL SETTING

Two well-differentiated tectono-sedimentary cycles, separated by a first-order unconformity, are evident in the Upper Carboniferous to Lower-Middle Triassic of the Southern Alps domain (e.g., Italian IGCP 203 Group, 1986; Cassinis *et al.*, 1988, 2012 and references therein; Massari *et al.*, 1988, 1994). In the Dolomites area (Fig. 1), the Lower Permian volcano-sedimentary megasequence is unconformably overlain, after a marked stratigraphic gap of over 10 Ma, by the alluvial red beds of the Gröden/Val Gardena Formation (Fig. 2), which form the basis of the second megacycle. The sedimentary development of this megacycle was driven by thermal subsidence (Massari and Neri, 1997), and is evidenced by widespread interfingering of continental and shallow-marine facies. Because of the cooling of the crust, sedimentation of the Val Gardena Sandstone was laterally extensive and shallow-marine deposits of the Bellerophon Formation prograded stepwise westwards on a very gentle ramp. According to Massari *et al.* (1994) and Massari and Neri (1997), the Upper Permian megacycle continues up to the overlying Triassic, including the Werfen Formation (Induan–Olenekian *p.p.*; Fig. 3) up to the Lower Anisian shallow-water carbonates of the Lower Serla Formation (latest Olenekian – early Anisian). The marine transgression of the Neotethys to the west took place in several third-order sequences, ranging from coastal-plain environments with sabkha evaporites to shallow-shelf carbonates of the Bellerophon Formation. After the end-Permian mass extinction, the mixed shallow-marine carbonates and terrigenous sediments

Fig. 2. Generalized stratigraphic section of the Val Gardena Sandstone and Bellerophon formations at the Bletterbach Gorge, Redagno (redrawn from Ceoloni *et al.*, 1986). Fish outline marks the position of the *Undichna* discovery.

of the Werfen Formation were deposited during a long-lasting biogenic recovery period that lacked carbonate-producing organisms. The first Triassic carbonate platform was only established in the early Anisian (Lower Sarl/Serla Formation), and its rocks mark the top of the second megacycle (De Zanche *et al.*, 1993; Gianolla *et al.*, 1998; Gianolla and Jacquin, 1998; Neri *et al*., 2007; Stefani *et al.*, 2010).

Fig. 3. Generalized stratigraphic section of the Werfen Formation (not to scale; slightly modified from Broglio Loriga *et al*., 1983; Neri, 2007). Fish outline marks the position of the *Undichna* discovery.

Val Gardena Sandstone

The Val Gardena Sandstone/Grödner Sandstein (Richtofen, 1860) (VGS) (Figs 1, 4) is a succession of Late Palaeozoic continental red beds, cropping out from the Giudicarie Valleys to the West and the Carnia area to the East, up to the border with Slovenia. The facies associations identified in the Val Gardena Sandstone indicate a fluvial-alluvial regime subject to rapid and erratic discharge fluctuations including alluvial fan through braided-stream and point-bar sequences, which show a final transition into a network of terminal fans of the distributaries of a fluvial system, encroaching on coastal-sabkha mud flats (Massari et al., 1988, 1994; Massari and Neri, 1997). The lowermost part of the Val Gardena Sandstone represents exclusively terrestrial strata composed of stacked upward-fining cycles (Massari et al., 1994), starting with coarse-grained sandstones or conglomerates at their bases that grade into shaly sandstone and siltstone towards the top. Conglomerate and sandstone are followed upward by reddish to locally variegated shaly siltstone to silty sandstone (Fig. 4B). The Val Gardena Sandstone red beds are laterally and upwardly replaced by the shallow-marine Bellerophon Formation related to the westward Palaeothethys transgression (Massari et al., 1988, 1994; Massari and Neri, 1997; Kustatscher et al., 2017), which in turn is overlain by the Low-er Triassic Werfen Formation (Massari et al., 1988, 1994; Cassinis et al., 2012). The Bellerophon Formation gives way from gypsum-bearing sabkha sequences, through lagoonal marls and dolomites, to shallow-shelf fossiliferous limestones. Generally, this upper unit highlights an overall transgressive trend.

The age of these continental deposits has been discussed widely because of the poor chronological significance of a large number of fossils, which do not allow very precise dating. Both the rich tetrapod footprint assemblages, which are very common and well known in the Bletterbach outcrops (e.g., Leonardi, 1951; Leonardi et al., 1975; Conti et al., 1977; Ceoloni et al., 1988; Valentini et al., 2007, 2009; Bernardi et al., 2015; Citton et al., 2016; Marchetti et al., 2017c), and the palaeobotanical and palynological associations (Kustatscher et al., 2012, 2014 and references therein; Bauer et al., 2014) are typical of Lopingian time. Other fossils include fish casts (Conti et al., 1975), invertebrate traces, cephalopods and coprolites (Conti et al., 1977) and insect herbivory (Labandeira et al., 2016).

The two Permian specimens described in this paper occur in tabular, red and grey, fine-grained sandstone and mudstone of the Val Gardena Sandstone in the Bletterbach section and belong to the facies associations, interpreted as formed in coastal mud flats (Massari et al., 1994), which preserve the most abundant and diverse tetrapod

Fig. 4. *Undichna*-bearing outcrops of the Upper Permian and Lower Triassic in the Dolomites. **A.** Lower-middle part of Werfen Formation (Lower Triassic) at Passo Valles. Smb: Siusi member; Gomb: Gastropod Oolite member; Cmb: Campil member. **B.** Upper Val Gardena Sandstone Formation (Upper Permian) in the Bletterbach Gorge. **C.** Muddy-silty, *Undichna*-bearing layers with load structures in the upper part of the Campil member (Lower Triassic) at Passo Valles. **D.** Medium-scale slump structures in the Campil member (Lower Triassic) at Passo Valles.

track ichnoassociation (e.g., Marchetti *et al.*, 2017c). The Bletterbach Gorge is undoubtedly one of the best localities of the Dolomites, where the Val Gardena Sandstone spectacularly crops out and where also the transition of this formation to the carbonates and evaporites of the Bellerophon Formation is very well exposed. This section was extensively studied, with regard to its sedimentology, stratigraphy and palaeontology (e.g., Ceoloni *et al.*, 1986; Conti *et al.*, 1997; Massari *et al.*, 1988, 1994; Cassinis *et al.*, 1999, 2012; Kustatscher *et al.*, 2017; Marchetti *et al.*, 2017c). Recent reviews dealt with the terrestrial palaeoenvironment and biota in the Bletterbach Gorge, particularly with regard to the palaeobotany (Kustatscher *et al.*, 2012, 2014, 2017) and the vertebrate palaeontology (Bernardi *et al.*, 2017; Marchetti *et al.*, 2017c).

Werfen Formation (Campil member)

The overlying Werfen Formation (latest Permian to late Olenekian) (Figs 3, 4) consists of a strongly variable sequence of mixed terrigenous siliciclastic and carbonatic lithofacies, organized in transgression/regression cycles, differing in order and frequency. For detailed descriptions of lithology and biostratigraphy, see Broglio Loriga *et al.* (1983, 1990). These authors introduced a division of the Werfen Formation into nine informal members (Tesero, Mazzin, Andraz, Siusi, *Gastropodenoolith*, Campil, Val Badia, Cencenighe, San Lucano). This formation is mostly shallow marine, although minor, subaerial episodes within the framework of transitional continental-marine environments do occur in some of its members (Broglio Loriga *et al.*, 1983; De Zanche *et al.*, 1993; Neri *et al.*, 2007). This is the primary reason why the Lower Triassic of the Southern Alps is characterised by the scarce presence of continental vertebrates, a factor that is undoubtedly linked to environmental conditions (palaeogeography), which did not favour the permanence of complex and consistent biotas in the region (Avanzini *et al.*, 2011). Nonetheless, Avanzini and Mietto (2008) noted that vertebrate tracks (*Rhynchosauroides palmatus* Lull, 1942 and *R. schochardti* Rühle Von Lilienstern, 1939) are present in the upper three members of the formation (Campil, Cencenighe and San Lucano members). They were found near Recoaro, in Val Gardena (Bulla/Pufels), and in Val Travignolo (Conti *et al.*, 2000; Mietto, 1986; Avanzini and Mietto, 2008; Avanzini *et al.*, 2011). Invertebrate trace fossils are relatively abundant in the Werfen Formation and bear witness to the different recovery phases of the ichnoassociation after the PT extinction (e.g., Twitchett and Wignall, 1996; Hofmann *et al.*, 2011; Baucon and Neto de Carvalho, 2016)

The Campil member consists of red siltstone and sandstone deposited on a shallow marine shelf (Broglio Loriga *et al.*, 1983; Broglio Loriga *et al.*, 1986 in Italian IGCP Project 203, 1986). This member conformably overlies the Gastropodenoolith member without any major change in the depositional pattern. It differs from the underlying unit only in lithology as it is almost completely made of terrigenous sediments; however, sparse calcarenite layers (bivalve packstone, oolitic grainstone, commonly with some terrigenous content), do occur (Broglio Loriga

et al., 1990). The typical depositional theme is represented by wave-dominated, shallowing-up sequences consisting of mudstone-dominated, mixed and sandstone-dominated lithofacies (Broglio Loriga *et al.*, 1986, 1990; Neri, 2007; Hofmann *et al.*, 2015).

The fossil invertebrates of the lower Campil member does not substantially differ from that of the underlying unit, whereas in the upper part there is a remarkable increase in the occurrence of pectinids and other peculiar bivalves (Broglio Loriga *et al.*, 1990; Neri, 2007; Neri *et al.*, 2007; Hofmann *et al.*, 2015). Also, in the upper part of the unit, the trace fossil *Asteriacites* records the occurrence of ophiuroids (*Preaplocoma* sp.; Broglio Loriga *et al.*, 1990). The Campil member shows an abundant trace fossils characterized by excellent preservation and low diversity. Documented ichnotaxa include *Asteriacites lumbricalis*, *Gyrochorte comosa*, *Diplocraterion habichi* and *Planolites beverleyensis* (Baucon and Neto de Carvalho, 2016). According to Brandner *et al.* (2009), *Diplocraterion*, undetermined burrows, micro-ripples and wrinkle structures are recurrent in the Campil member. Most typical are "Kinneyia" structures, millimetre-scale winding ridges resembling small-scale interference ripples, usually preserved on the flat upper surfaces of siltstone or sandstone beds. As suggested by Porada and Bouougri (2007), these structures may have formed underneath microbial mats. In the sandy lithofacies, different kinds of parallel and cross-laminations occur; in the thicker strata, a coarsening-upwards microsequence with parallel lamination at the base, then hummocky cross-lamination and wave ripples at the top, can be also observed (Broglio Loriga *et al.*, 1983). The Campil member is considered mostly Smithian (early Olenekian) (Nammalian of Broglio Loriga *et al.*, 1990 and references therein; Twitchett, 2000), mainly on the basis of the presence of *Costatoria rubrotunda* (Bittner).

The *Undichna* sample was recovered during a field trip in the Passo Valles area, *in situ* in the upper part of Campil member (Figs 3, 4A). The *Undichna*-bearing deposits consist of grey siltstones. These deposits are interpreted as formed in a very shallow-marine and muddy setting above the wave base.

MATERIAL AND METHODS

During geological surveys of the Upper Permian-Lower Triassic successions of the Southalpine, specimens of *Undichna* were found in two different sections and units. Two slabs from the Val Gardena Sandstone (Late Permian) show impressions of fish trails and both are in association with vertebrate tracks. These specimens are stored at the Museum of Palaeontology of the University "La Sapienza" of Rome (acronym UR-NS) and in the Museum of Geology and Palaeontology of the University of Padua (acronym MGP-PD). Specimen UR-NS 34/105 is a reddish, parallel-laminated, fine-grained sandstone slab with small tetrapod tracks and ripple marks, preserved in convex hyporelief, and comes from the fine-grained deposits of the Bletterbach section (Fig. 2). It was collected by the Conti-Nicosia team during their palaeontological surveys in the eighties-nineties. Specimen MGP-PD 26594 is a grey, fine-grained sand-

stone with tetrapod tracks and tail impressions, preserved in concave epirelief, collected by P. Leonardi in the fifties from the same locality and stratigraphic interval. This is also the slab containing the holotype of ?*Nanopus grimmi* and *Prochirotherium permicum* Leonardi, 1951; which are small tetrapod tracks preserved in convex hyporelief.

Another slab, a grey siltstone with trace fossils preserved in convex hyporelief (Fig. 3) from the Campil member (Lower Triassic), is stored in the Dipartimento di Scienze della Terra e dell'Ambiente of the University of Pavia (specimen UPTF-CAM 1).

The parameters utilized for the measurements are those proposed by Cardonatto and Melchor (2014).

SYSTEMATIC PALAEOICHNOLOGY

Ichnogenus *Undichna* Anderson, 1976

Undichna cf. *quina* Trewin, 2000

Fig. 5

Locality: Bletterbach Gorge (Aldino-Redagno, Bolzano). Val Gardena Sandstone (Italy).
Material: UR-NS 34/105, convex hyporelief.
Description: The trail consists of a regular succession of a pair of sinusoidal, interwined, in-phase, horizontal waves. The wavelength is 98.9–100–121.1 mm. The maximum amplitude of pectoral or pelvic fin wave is 24.4–33.3 mm. The pelvic fin wave cuts the pectoral fin wave and has a slightly larger amplitude. The course of the trail is partially interrupted at two different points. The trail seems to lack the outer waves and the caudal trail. On the same surface are isolated tetrapod footprints (cf. *Procolophonichnium* isp.) and parallel ripple crests.
Remarks: *Undichna quina* was first introduced by Trewin (2000); the general morphology of the trail from the Val Gardena Sandstone is very similar to those figured in numerous studies because of the in-phase, interwined, horizontal waves (e.g., Trewin, 2000; Lucas *et al.*, 2004; Minter and Braddy, 2006; Fillmore *et al.*, 2011; Cardonatto and Melchor, 2014 and so on). Compared with complete specimens (e.g., the *U. quina* from the continental Abrahamskraal Formation of South Africa, shown in Fig. 8A), the trail from the Val Gardena Sandstone presents some differences; in the slab, only a side of the trail is impressed and is composed of impressions of the pectoral and pelvic fins. The caudal fin impression is also lacking. The only *Undichna* ichnospecies with intertwined and in-phase waves, without grooves are *U. gosiutensis*, *U. insolentia* and *U. quina*. However, *U. insolentia* is a very complex trace and when incomplete is characterized by at least four parallel waves (e.g., Anderson, 1976); thus it can be excluded from consideration. In terms of its morphology, the trail from the Val Gardena Sandstone seems to show a strong similarity with *U. quina* (Trewin, 2000, figs 3, 4; Minter and Braddy, 2006, fig. 2K; Fillmore *et al.*, 2011, fig. 3). Following the interpretation of Minter and Braddy (2006) about the synonymy of *U. gosiutensis* with *U. quina*, but having an incomplete trackway, the present authors assign this material to *U.* cf. *quina*.

Undichna bina Anderson, 1976

Fig. 6

Locality: Bletterbach Gorge (Aldino-Redagno, Bolzano). Val Gardena Sandstone (Italy).
Material: MGP-PD 26594, concave epirelief.
Description: The trail consists of one pair of partially deformed, parallel, in-phase and slightly sinusoidal waves. The course of the trail is interrupted by crossing of the grooves, probably a vertebrate tail impression. In fact, some of them are associated with tetrapod tracks (*Rhynchosauroides* isp.).
Remarks: This impression is a very simple trail, the simpler of ichnospecies described by Anderson (1976) and despite its incompleteness, the peculiarities of the ichnospecies can be clearly observed. This trail consists of one pair of clearcut lines, a constant distance apart. These usually follow a sinusoidal or slightly asymmetrical, sinusoidal course, but in places they may undulate in an irregular way; they are never entirely straight (Anderson, 1976).

Partial preservation of the trail may result in potential confusion with invertebrate trackways or with vertebrate tail impressions; yet the lack of clearly associated autopodia impressions and the parallelism support a fish origin. Higgs (1988) provided a discussion of *U. bina* and Minter and Braddy (2006, tab. 1) analysed its temporal and geographical distribution.

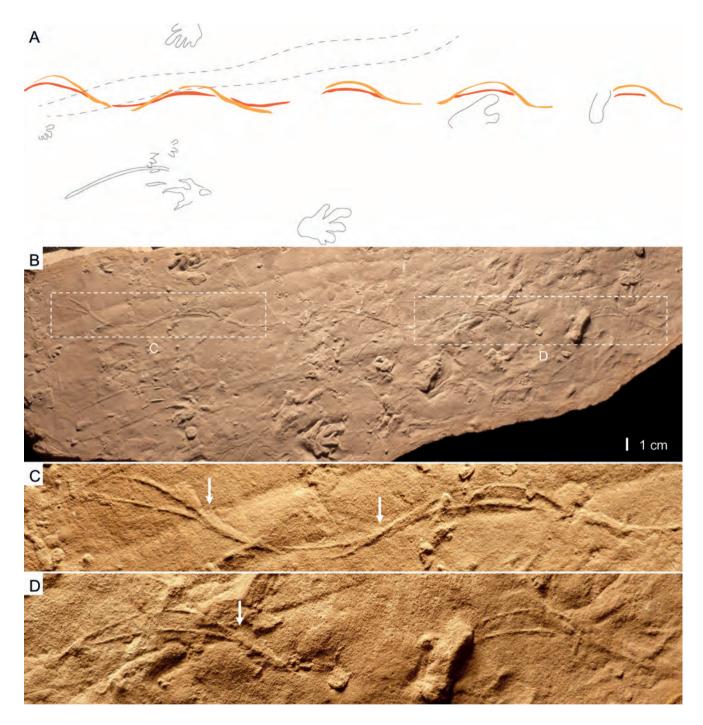*Undichna* cf. *britannica* (Higgs, 1988)

Fig. 7

Locality: Passo Valles (N Italy). Werfen Formation (Campil member).
Specimen: UPTF-CAM 1, convex hyporelief.
Description: An incomplete trail that consists of intermittent components, characterized by a pair of a partial, horizontal, intertwined, out-of-phase and sinusoidal waves. In addition, probably the ventral fin impressed an outer short, slightly oblique trail. Measurements of the individual components are difficult; the almost complete trail (Fig. 6B, arrow) has a wavelength of about 39 mm.
Remarks: Notwithstanding the incompleteness of the trail, the fairly-good preservation of at least two portions of the slab, allows further discussion. Three ichnospecies of *Undichna* are seen in the out-of-phase sinusoidal waves: *U. britannica*, *U. consulca* and *U. radnicensis*. The main difference between these ichnospecies is in the morphology of the outer grooves. In fact, in *U. consulca*, the furrows impressed by the fish's belly (Higgs, 1988) are evident, whereas in *U. britannica* these are not present. Also, the development of the outer grooves is different: straight in *U. consulca* and short and oblique in *U. britannica*. Turek (1989) formalized the new ichnospecies *U. radnicensis*, a fish trail very similar to *U. britannica*, but one in which the outer grooves are more continuous (Minter and Braddy, 2006). In the slab from Campil member, the general morphology of the fish trail is similar to that of *U. britannica* (see Buatois and Mángano, 1993, 1994) and the complete and continuous *U. britannica* from the continental Abrahamskraal Formation of South Africa shown in Fig. 8B, C). Howev-

Fig. 5. *Undichna* cf. *quina*. UR-NS 34/105, Val Gardena Sandstone Formation, Lopingian, Italy. **A.** Interpretive drawing. In red, the anterior lateral fin trace and in yellow, the posterior lateral fin trace (larger amplitude; cuts the anterior trace). The two sinusoids are roughly in phase. Note the tetrapod footprints and the parallel ripple crest – dashed lines. **B.** Photograph, convex hyporelief. **C, D.** Enlargements of portions of the trace; arrows highlight the sinusoid superimposition.

er, the incompleteness of UPTF-CAM 1 prevents a definitive classification. Therefore, it is referred as *U.* cf. *britannica*.

STRATIGRAPHY AND THE TRACEMAKERS

Minter and Braddy (2006) documented the chronostratigraphic distribution of known *Undichna* ichnospecies. The first appearance of *U. quina* corresponds to the Late Carboniferous of Argentina (Cardonatto and Melchor, 2014), whereas the youngest is represented by its presence in the Jurassic (Gibert, 2001). Therefore, the Italian specimen of *U.* cf. *quina* (Lopingian) falls within this stratigraphic range.

The oldest record of *U. bina* is from the Early Carboniferous of eastern Canada (Cameron *et al.*, 1998) and the youngest one from the Late Cretaceous of Argentina (Cardonatto and Melchor, 2014, tab. A.2). The discovery in the Val Gardena Sandstone together with *U. quina*, constitutes

Fig. 6. *Undichna bina*. MGP-PD 26594, Val Gardena Sandstone Formation, Lopingian, Italy. **A.** Photograph, concave epirelief. Arrows indicate the trace fossil. **B.** Interpretive drawing. The trace fossil is highlighted in yellow. Note the slight sinuosity and the two parallel traces. Note tetrapod footprints and supposed tail impressions on the same slab.

the oldest fish trail recorded in this area so far. Both were found in marginal marine, alluvial palaeoenvironments.

Undichna britannica has an extensive chronological distribution, from the Late Mississippian of the USA (Fillmore *et al.*, 2011) until the Holocene (Gibert *et al.*, 1999). Most

records occur in the Carboniferous to Middle–Late Triassic, with a gap in the Early Triassic and in the Jurassic. The discovery of *U.* cf. *britannica* in the Werfen Formation of the Dolomites potentially covers the Early Triassic gap, and it also constitutes the first Mesozoic record from Italy, before

Fig. 7. *Undichna* cf. *britannica.* UPTF-CAM 1, Werfen Formation, Campil member, Lower Triassic, Italy. **A.** Photograph, convex hyporelief. Note the discontinuity of traces. **B.** Enlargement of A. Arrow indicates the intersection of out-of-phase sinusoidal traces.
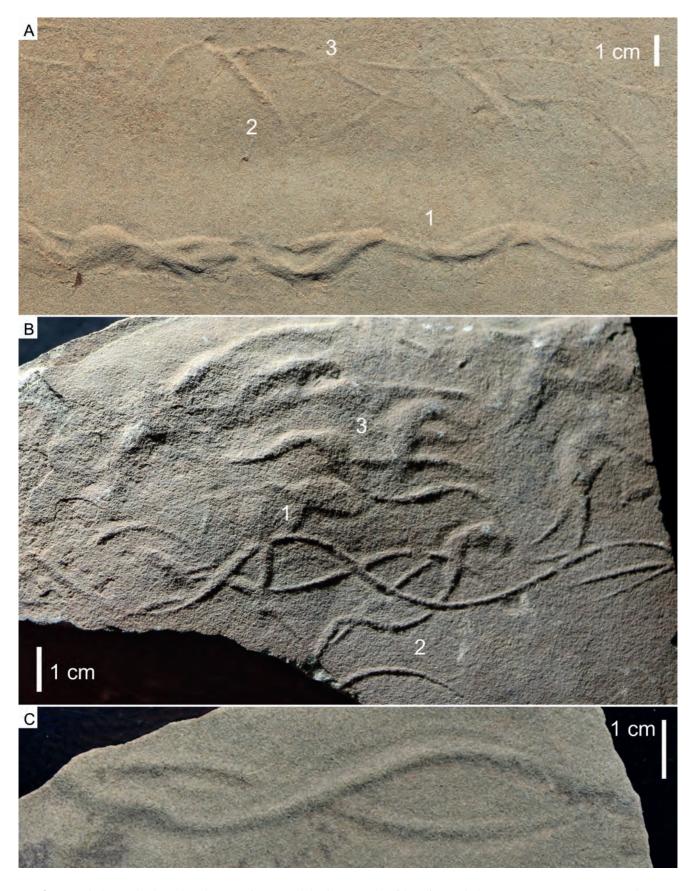
the only previous record of *Undichna* in the Southern Alps, the late Anisian *U. gosiutensis* documented by Todesco and Avanzini (2008). This represents also one of the rare occurrences of *Undichna* in fully marine environments (compare Minter and Braddy, 2006; Feng *et al.*, 2017).

As reported by Cardonatto and Melchor (2014), many potential trace makers could produce these trails. *Undichna bina* can be the impression of the pelvic or pectoral fins of palaeonisciforms (Anderson, 1976; Higgs, 1988; Trewin, 2000; Minter and Braddy, 2006), of flatfish (Lu, 2004), of chondroichthyes (in particular hybodont sharks) and of dipnoans, as well. In any case, the kind of fin, pectoral or pelvic, can indicate the locomotion type (anguilliform or subcarangiform). For *U. quina* and *U. britannica,* the most promising potential tracemakers are the palaeonisciforms with a subcarangiform locomotion type (Cardonatto and Melchor, 2014).

These observations have been supported by the fish impressions found in the Bletterbach area, which are supposed to be referable to palaeonisciforms or primitive holostei with small, even fins (Conti *et al.*, 1977). Besides, biomechanical analyses indicate that the fish, tracemakers of *Undichna*, must have been small in size (mostly less than 250 mm and up to 650 mm) in order to be preserved as a recognizable trail (Cardonatto and Melchor, 2014); this is consistent with the size of the fish impressions studied by Conti *et al.* (1975, 1977), ranging from 70 to 80 mm in length.

PALAEOECOLOGY

In the Palaeozoic of the Southern Alps, the only record of fishes corresponds to a petalodont tooth (*Petalodus ohioensis*, Safford 1853) from the Upper Carboniferous of the Carnic Alps (Dalla Vecchia, 1988) and to a large number

Fig. 8. *Undichna*, Abrahamskraal Formation, Guadalupian, South Africa. **A.** *Undichna quina*, GRAN 1, convex hyporelief; 1 – in-phase, deeply impressed, sinusoidal traces; 2 – out-of-phase trace with large amplitude; 3 – in-phase, shallow, sinusoidal traces. **B.** *Undichna britannica*. SAM-PT K 7877, convex hyporelief. Note the pairs of intertwined, out-of-phase, sinusoidal traces. Numbers are three different *U. britannica*. **C.** *U. britannica*. GRAN 2, convex hyporelief. Note the intersection of two sinusoidal traces that are opposite in phase.

(28 complete impressions and six fragmented) of unclassified fishes (palaeonisciforms or primitive holostei), reported in the upper part of the Val Gardena Sandstone in the Bletterbach Gorge (Fig. 2) by Conti *et al.* (1975). They occur on a tabular sandstone slab, where also tetrapod footprints (*Rhynchosauroides*) are preserved in convex hyporelief. These fish casts show an elongated and fusiform trunk and a maximum length of about 7–8 cm (for the complete description, see Conti *et al.*, 1975, 1977). These fishes are supposed to be adapted to different salinity conditions (Conti *et al.*, 1977).

The fish trail *Undichna* is recorded here for the first time in the Val Gardena Sandstone; and indicates oxygenated environments. The documentation of *U.* cf. *quina* and *U. bina* in the Bletterbach section expands the number of the components of the ichnoassociation that to date was composed only of tetrapod footprints and invertebrate trace fossils (Conti *et al.*, 1977; Marchetti *et al.*, 2017c). The tetrapod footprint ichnoassociation of the Val Gardena Formation recently was revised comprehensively (Marchetti *et al.*, 2017a, c) following anatomically related criteria that are crucial for a correct ichnotaxonomic and faunistic interpretation of the footprints (e.g., Voigt *et al.*, 2007; Marchetti *et al.*, 2017b). The *Undichna*-bearing layers include ten different tetrapod ichnotaxa (Fig. 9A): cf. *Batrachichnus* isp. (temnospondyl amphibian), *Capitosauroides* isp. (amphibian), *Dicyno-dontipus* isp. (cynodont therapsid), *Dolomitipes accordii* (dicynodont therapsid), cf. *Dromopus* isp. (neodiapsid), *Pachypes dolomiticus* (pareiasaurian parareptile), *Paradoxichnium problematicum* (archosauromorph neodiapsid), *Procolophonichnium tirolensis* (procolophonoid parareptile), cf. *Protochirotherium* isp. (archosauriform neodiapsid) and *Rhynchosauroides pallinii* (neodiapsid). This ichnoassociation is diverse and characterised by the predominance of neodiapsid and parareptile tracks, less common therapsid tracks and rarity of amphibian tracks, reflecting an ideal environment for the development of a complex trophic network (Bernardi *et al.*, 2017). The invertebrate trace fossils are not diverse and include *Rhizocorallium*, ?*Kouphichnium* and undetermined invertebrate burrows (Conti *et al.*, 1977). *Rhizocorallium* is indicative of brackish-water to fully marine conditions (Conti *et al.*, 1977; Knaust, 2013), ?*Kouphichnium* is typical of coastal environments and the invertebrate burrows indicate oxygenated water.

The lithofacies (tabular, fine-grained, laminated sandstone and mudstone) is indicative of medial to distal floodplain environments, in a marginal marine setting, because of the lagoon interfingering lithofacies of Bellerophon Formation. Thus, it can be hypothesized that a freshwater to brackish marginal marine environment occurred. Interestingly, both specimens studied preserve several small tetrapod footprints on the same surface and UR-NS 34/105 show clear
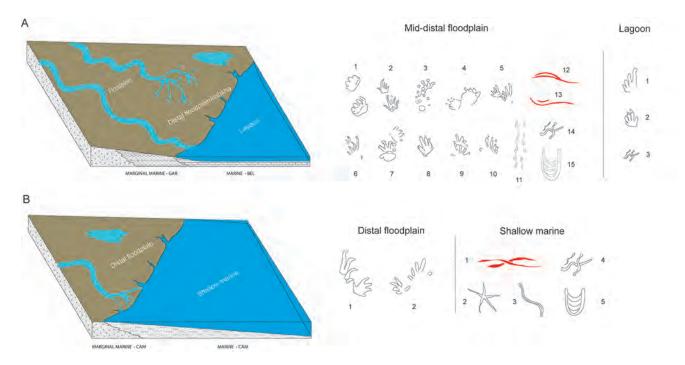

Fig. 9. Idealized palaeoenvironmental reconstructions of the Dolomites in the Late Permian and Early Triassic. **A**. Late Permian scene: depositional setting of the Val Gardena Sandstone Formation. Ichnoassociation in mid-distal-floodplain palaeoenvironments (1–15). 1 – *Pachypes dolomiticus*, 2 – *Procolophonichnium tirolensis*, 3 – *Dolomitipes accordii*, 4 – *Dicynodontipus* isp., 5 – *Rhynchosauroides pallinii*, 6 – cf. *Dromopus* isp., 7 – cf. *Protochirotherium* isp., 8 – *Paradoxichnium problematicum*, 9 – *Capitosauroides* isp., 10 – cf. *Batrachichnus* isp., 11 – cf. *Kouphichnium* isp., 12 – *Undichna quina*, 13 – *Undichna* cf. *bina*, 14 – invertebrate burrows, 15 – *Rhizocorallium* isp. Ichnoassociation in lagoon palaeoenvironments (1–3). 1 – cf. *Capitosauroides* isp., 2 – *Paradoxichnium* isp., 3 – invertebrate burrows. **B**. Early Triassic scene: depositional setting of the Werfen Formation, Campil member. Ichnoassociation in distal-floodplain palaeoenvironments (1–2). 1 – *Rhynchosauroides schochardti*, 2 – *Rhynchosauroides palmatus*. Ichnoassociation in shallow-marine palaeoenvironments (1–5). 1 – *Undichna* cf. *britannica*, 2 – *Asteriacites lumbricalis*, 3 – *Gyrochorte comosa*, 4 – *Planolites beverleyensis*, 5 – *Diplocraterion habichi*.

parallel ripple marks. Both features support a very shallow environment, subject to sudden flooding and drying. Mud cracks and vertisols are known from these lithofacies, and indicate drying events and a semi-arid climate, consistently with the palaeobotany (Massari *et al.*, 1994; Kustatscher *et al.*, 2012). Therefore, the medial-distal floodplain environments at the transition between Val Gardena Sandstone and the shallow marine Bellerophon Formation show direct and indirect proofs of fish occurrences in very shallow, oxygenated and brackish water in a semi-arid environment, characterized by a complex trophic network.

The interfingering lagoon lithofacies (Fig. 9A) could represent an environment more hostile to life evidenced by the occurrence of several opportunistic and non-specialized invertebrates in the basal strata of Bellerophon Formation (e.g., Broglio-Loriga *et al.*, 1988; Venturini, 1990). Nevertheless, invertebrate burrows were also observed in this lithofacies. Therefore, at least occasionally the lagoon was oxygenated and probably permitted the access of fishes to the sea (Marchetti *et al.*, 2017a, in a different locality). Tetrapod footprints associated with the lagoon lithofacies are rarer and less diverse (cf. *Capitosauroides* isp. and *Paradoxichnium* isp.; Marchetti *et al.*, 2017a) (Fig. 9A). The producers of these tetrapod footprints may have been better adapted to these conditions; this would explain the different trace fossil composition, compared to the floodplain ichnoassociation.

Following Accordi (1955, 1956), the Lower Triassic Werfen Formation preserves rare fish remains, attributed to *Semionotiforms holostei*, but in more recent times, other authors consider that these forms belong to the Permian Bellerophon Formation (Sirna *et al.,* 1994; Blieck *et al.*, 1997). Leonardi (1960, 1967) report the presence of "Semionodontidae" indet. (Semionotiformes, Osteichthyes) from the base of Campil member in Ziano di Fiemme.

The silty-sandy lithofacies of the Campil member can be referred to a mostly sub-tidal, well oxygenated environment with sandy shoals, on a very shallow seabed, but above the fair-weather wave base (Broglio Loriga *et al.*, 1983; Figs 4C, D, 9B), because of the presence of abundant interference wave ripples, hummocky cross-stratifications and even laminations. The trace fossil composition and the bioturbation style of the Campil member indicate a marginal marine palaeoenvironment, ranging from intertidal to shallow subtidal settings to supratidal at its top (Broglio Loriga *et al.*, 1983).

The occurrence of *Undichna britannica* and the associated sedimentary structures are consistent with a well-oxygenated, shallow environment, in agreement with the presence of abundant invertebrate trace fossils. However, the invertebrate ichnoassociation is not very diversified, including only four ichnospecies (*Asteriacites lumbricalis*, *Gyrochorte comosa*, *Diplocraterion habichi* and *Planolites beverleyensis*) (Fig. 9B) and reflects stressed palaeoenvironmental conditions (Zonneveld, 2011; Baucon and Neto de Carvalho, 2016)**.** The discovery of tetrapod footprints in the upper Werfen Formation (the neodiapsid tracks *Rhynchosauroides schochardti* and *Rhynchosauroides palmatus*; Avanzini and Mietto, 2008, in different localities) is consistent with a shallow-marine environment with occasional or local emersions (Fig. 9B).

CONCLUSIONS

These new discoveries represent the first ichnological evidence of fish swimming activity in the Upper Permian and Lower Triassic units of the Southern Alps. They also are significant in providing new data for a more accurate palaeoenvironmental characterization of the sedimentary units. In particular, the Upper Permian fish trails occur in deposits that were formed in very shallow, calm, brackish and oxygenated distal floodplain and marginal marine environments, in association with abundant and diverse tetrapod tracks and non-diverse invertebrate trace fossils. Conversely, the Lower Triassic *Undichna* were produced on an intertidal to subtidal calm, shallow, marine ramp that also preserved abundant, but not diverse, invertebrate trace fossils.

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