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The Middle Triassic palaeontomofauna of Monte San Giorgio with the description of *Merithone laetitiae* (†Permithonidae) gen. et sp. nov.

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Abstract

The Triassic is considered a crucial period for the establishment of the modern insect fauna and fossil records from this period are fundamental for understanding the real impact that the end Permian Mass Extinction events had on these animals. Here, we review the insect fossils from one of the main deposits of this period in the world, Monte San Giorgio, which is considered one of the nine main insect Fossillagerstätten. In this Lagerstätte, located on the border between Switzerland and Italy, a total of 273 fossil insects have been collected in five localities. The fossils found in Val Mara site D, one of the two richest insect fossils sites of Monte San Giorgio, present peculiar features, such as extraordinary sizes and phosphatisation of internal tissues revealing fine internal details. In contrast, the Val Mara site VM 12 fossil record (248 specimens) is dominated by small to medium size insects, usually almost intact, preserving details such as setae on wings and compound eyes. Besides these exceptional features, these fossil insects are of extreme evolutionary importance, since they represent the first or the last occurrence for their lineage. In this regard, their use to calibrate nodes in a phylogenomic dating analysis led to backdating the origin of many insect lineages, including Diptera and Heteroptera. Up to now, a total of five species from Monte San Giorgio have been formally described, belonging to the orders Archaeognatha (†Monura and Machilidae), Ephemeroptera, Hemiptera (Tingidae) and Coleoptera (Adephaga). A further species, *Merithone laetitiae* (†Permithonidae) gen. et sp. nov., whose fossil is included among the recent findings in Val Mara site VM 12, is described in the present work.

Introduction

Triassic relevance for the understanding of the evolution of modern insect faunas

The Triassic is considered a crucial period for the establishment of modern insect fauna and therefore it is essential to study the fossils of this period to understand insect evolution (Benton, 2016; Zheng et al., 2018). It is believed that a diversity drop and a turnover of faunal composition occurred in this period (Shuang-Mao et al., 2023), with some of the Palaeozoic lineages such as †Monura and †Paleodyctioptera disappeared (Grimaldi & Engel, 2005; Labandeira & Sepkoski, 1993) while others, such the holometabolans, experienced an evolutionary burst (Misof et al., 2014; Montagna et al., 2019; Zheng et al., 2018). Supposedly, this faunal turnover was mainly promoted by the eco-space left vacant after the end Permian Mass Extinction event (EPME), the most severe biotic extinction event of the Phanerozoic (Raup, 1979; Song et al., 2013). However, recent studies raise

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the question if continental faunas, and in particular the insects, were really so dramatically affected by this event (Montagna et al., 2019; Nowak et al., 2019; Schachat & Labandeira, 2021) and hypothesized that other global-scale events (such as the Carnian Pluvial Episode, ~ 234 to ~232 Ma; Late Triassic) might have mostly driven an insect turnover from the Palaeozoic to the Mesozoic, as well as the establishment of the modern fauna (Montagna et al., Submitted). In this context, further excavations and the careful analysis of insect fossils from Triassic sites is essential for shedding light on their evolutionary history. Among the sites of interest in this regard is the Monte San Giorgio UNESCO's World Heritage Site, located on the border between Switzerland and Italy (Fig. 1A). Following the findings of the last 24 years, this site may be listed among the nine most important Triassic fossiliferous sites in the world for insects (Montagna et al., Submitted; Schachat & Labandeira, 2021).

Geological setting at Monte San Giorgio

Monte San Giorgio's Middle Triassic carbonate succession is celebrated for the remarkably preserved fossils of fishes and marine reptiles found over the last one hundred years (e.g., Rieppel, 2019). Hence, it was awarded the rank of an UNESCO World Heritage site (Switzerland-Italy Fig. 1A). The unique sedimentary conditions of this area are the result of a long-term transgression leading to intermittent dysoxic-anoxic bottom water (Bernasconi, 1994; Stockar et al., 2013; Tintori, 1992). The Middle Triassic succession (Fig. 1B) starts with fluvio-deltaic deposits over Lower Triassic clastic layers. It is overlain by upper Anisian sediments indicating the progressive transgression of a shallow epicontinental sea and the related expansion of carbonate platforms. In the late Anisian and the Ladinian, a 614 m thick sequence of carbonates and fine clastic sediments, the Besano Formation, San Giorgio Dolomite, and Meride Limestone, formed in an intraplatform basin. The lower Meride Limestone contains fossil-rich intervals with unique vertebrate assemblages ("Cava inferiore beds", "Cava superiore beds" and "Cassina beds", e.g., Sander, 1989; Furrer, 1995; Stockar, 2010). The upper Meride Limestone exhibits alternating micritic limestone and marlstone including the Sceltrich beds, which are currently studied (Stockar et al., 2013). The uppermost part, the "Kalkschieferzone" (Senn, 1924), is a 120 m thick unit with diverse fossils (e.g., Furrer, 1995; Lombardo et al., 2012; Wirz, 1945) reflecting a shallow lagoon environment with seasonal salinity variations (Tintori, 1990). During Ladinian times, the region experienced monsoonal circulation (Preto et al., 2010), leading to seasonal variations and density stratification in the hypersaline lagoon (Furrer, 1995).

Results

Discoveries of insect fossils at Monte San Giorgio

At present, the palaeontomofauna of Monte San Giorgio consists of 273 fossils collected in five sites. The oldest fossiliferous site, in geological terms, is represented by the Cava Superiore beds (Lower Meride Limestone; 241.07 ± 0.13 Mya). It is a finely laminated limestone where fossils of a dragonfly (MCSN 4994) and a beetle (MCSN 4995) were collected in 1999 during excavations conducted by Palaeontological Institute and Museum of the University of Zurich and the Cantonal Museum of Natural History. A further, single, and partially phosphatized specimen (MCSN 8682) assigned to Polyneoptera was collected from the Sceltrich beds in 2019. The majority of the insect fossils known from Monte San Giorgio were collected within the Kalkschieferzone in Val Mara along the Gaggiolo River. Between 1997 and 2003, during excavations carried out by the University of Milan and Cantonal Museum of Natural History in Val Mara Lower Kalkschieferzone (239.51 ± 0.15 Mya) "Site D" (hereafter, Val Mara site D), 19 fossils belonging to six different insect orders were collected. Among them, four taxa have been formally described. Specifically, the bristletail *Gigamachilis triassicus* (Archaeognatha, Machilidae) (Montagna et al., 2017), the mayfly *Tintorina meridensis* (Ephemeroptera, Tintorinidae) (Krzeminski & Lombardo, 2001), the lace bugs *Archetingis ladinica* (Hemiptera, Tingidae) (Montagna et al., 2018), and the beetles *Praedodromeus sangiorgensis* (Coleoptera, Trachypachidae) (Strada et al., 2014) (Fig. 2).

In 2010, the excavations on Val Mara site VM 227 in the Upper Kalkschieferzone led to the discovery of three further insect fossils (MCSN 8343–8345) assigned to the extinct group of †Monura (Archaeognatha), and described as *Dasyleptus triassicus* (Bechly & Stockar, 2011) (Fig. 2). More recently (2020–2023), new excavations were conducted by the Cantonal Museum of Natural History in Val Mara site VM 12 (Upper Kalkschieferzone, dated ~ 239 Mya). These activities led to the discovery of a considerable number of fossil insects (248 specimens already prepared and studied plus further specimens not studied yet). Thus, this locality is by far the most prolific site with respect to insect fossils of the Monte San Giorgio region.

These fossils were attributed to 15 major insect lineages belonging to the following orders: †Monura, Odonata, Blattodea, Thysanoptera, Hemiptera, Psocodea, Hymenoptera, Neuropterida, Coleoptera, Trichoptera, Mecopteroidea, Mecoptera, Amphiesmenoptera, and Diptera (Montagna et al., Submitted). In addition, 29 individuals were assigned to *incertae sedis*. Among these fossils, a sawfly (Hymenoptera, Xyelidae) described by Montagna

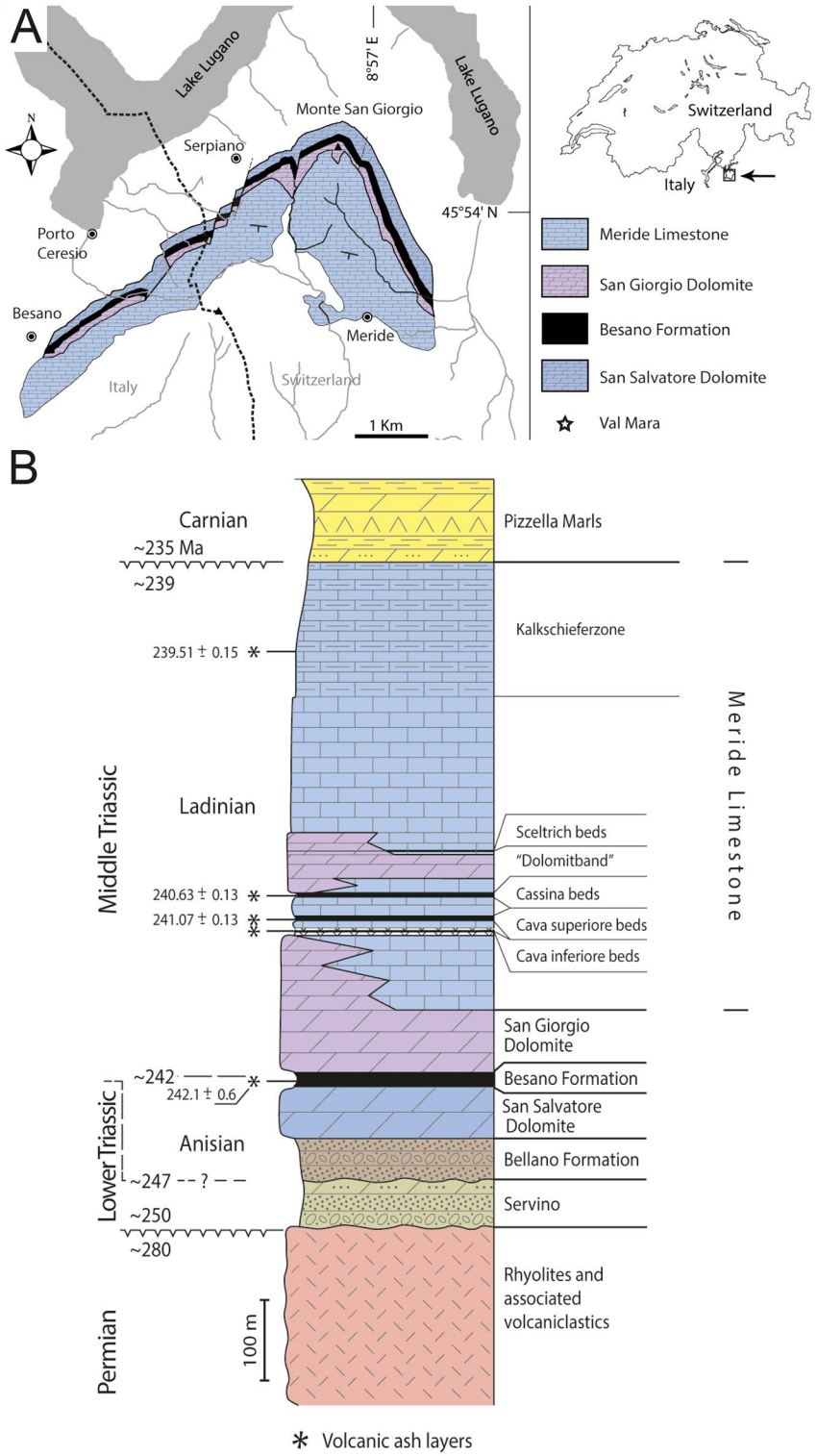

Fig. 1 Location of the Monte San Giorgio and stratigraphic section of the Middle Triassic sediments. **A** Map showing the location of Monte San Giorgio and the carbonate Anisian-Ladinian sequence. **B** Middle Triassic stratigraphic units of the Monte San Giorgio area. Stratigraphic column after Commissione scientifica transnazionale Monte San Giorgio 2014, modified. Single-zircon U–Pb ages of Meride limestone after Stockar et al., 2012

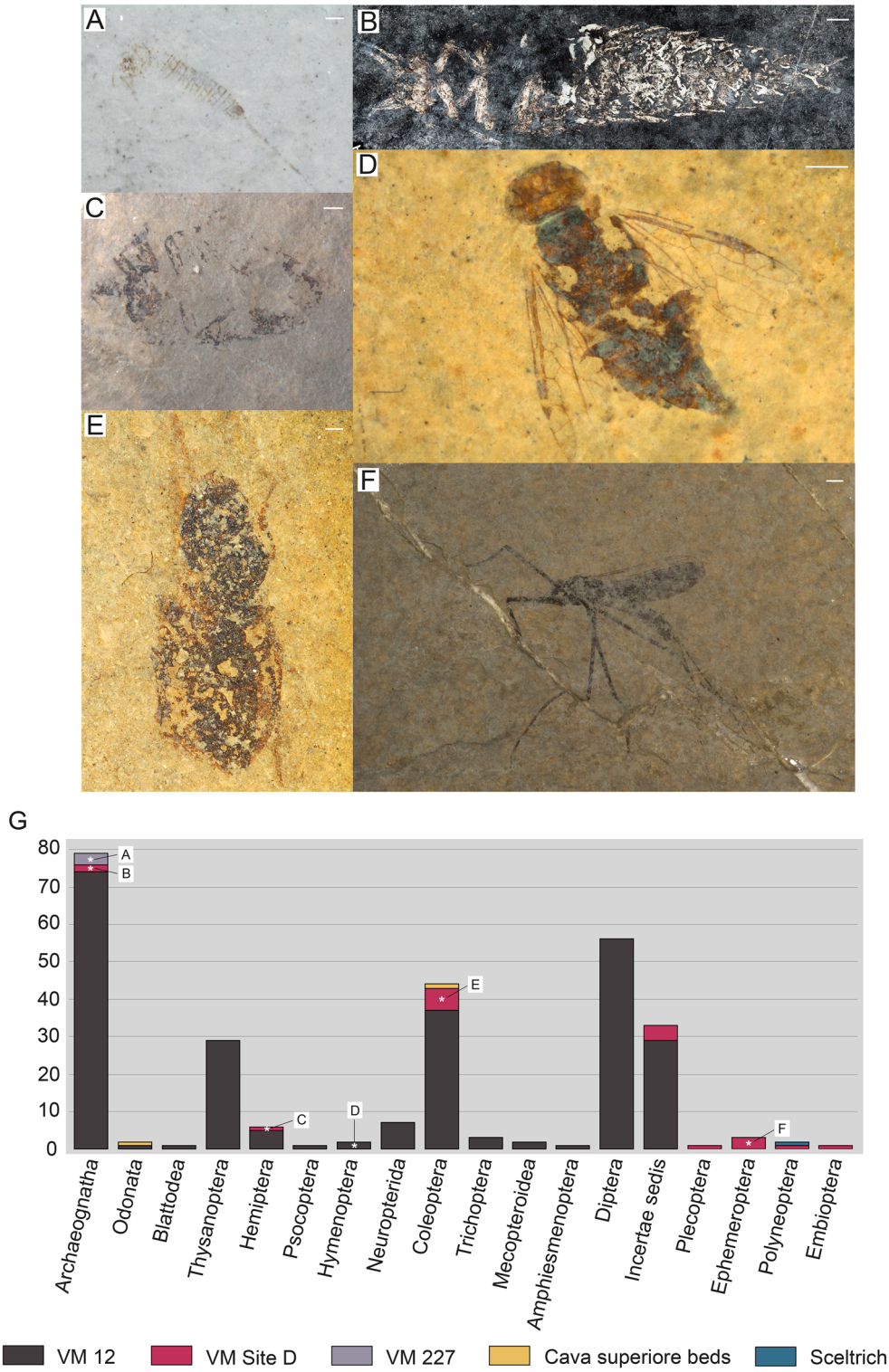

Fig. 2 Insect fossil findings in the five fossiliferous sites of Monte San Giorgio and described species. Species from Monte San Giorgio described until now: **A** *Dasyleptus triassicus* (Archaeognatha, †Monura, †Dasyleptidae) (scale bar 500 µm); **B** *Gigamachilis triassicus* (Archaeognatha, Machilidae) (scale bar 2 mm); **C** *Archetingis ladinica* (Hemiptera, Tingidae) (scale bar 1 mm); **D** Sawfly (scale bar 1 mm); **E** *Praedodromeus sangiorgensis* (Coleoptera, Trachipachidae) (scale bar 1 mm); **F** *Tintorina meridensis* (Ephemeroptera, Tintorinidae) (scale bar 1 mm). **G** Barplot showing the number of fossil findings per taxon at each fossiliferous site; asterisks followed by identification letters indicate the described species shown above

et al. (submitted) and a further new taxon remained *in litteris*. The latter is formally described in the present contribution.

Features of Monte San Giorgio insect fossils

The insect fossils collected in the five known sites of Monte San Giorgio present different modes of preservation as well as other different features that make them peculiar among the known Triassic fossils. The main differences occur between the insect fossils collected in the two richest insect fossils sites in the Kalkschieferzone of Monte San Giorgio, Val Mara site D and VM 12. In Val Mara site D, medium to very large fossils were recovered such as *Gigamachilis triassicus* with an estimated length of ~ 80 mm and the incomplete larva of a holometabolan of approximately 4 cm in length (Montagna et al., 2018, 2019), the majority of which are disarticulated and with limited preservation of fine external morphological details. The ecological drivers that promoted the evolution of the extraordinary size of these fossils remain unknown, although some hypotheses have been postulated (Montagna et al., 2018). Approximately one third of the fossils of this assemblage, and in particular those of the groups with a lightly sclerotised exoskeleton, are completely or partially phosphatized (Strada et al., 2014). The phosphatisation of the organic matter of the insects is a bacteria-mediated process occurring in anoxic conditions, during which a microbial film is deposited on decaying animal tissues and prevents phosphate diffusion (Briggs & Kear, 1993, 1994). As a consequence of phosphatisation, the internal tissues and organs of some fossils collected in site D are exceptionally preserved. In particular, *G. triassicus* preserves components of the central nervous system such as pairs of ventral nerve chord ganglia and part of the optic lobes (Montagna et al., 2018; Fig. 2). A grasshopper-like fossil preserves tubular structures, identified as Malpighian tubules in the distal part of its abdomen. Thanks to these findings, the components of the central nervous system and Malpighian tubules have been found for the first time in compression fossils of terrestrial arthropods, thus emphasising the worldwide relevance of the Monte San Giorgio site. Both the size of Val Mara site D fossils (medium to large) and their preservation status (some of them are disarticulated and phosphatized) are compatible with a rapid transport of their dead body during high energy events to the depositional basin, in this case a shallow lagoon close to a carbonate platform. Moreover, the high ratio between insect specimens and orders registered for the Val Mara site D, including representatives of different guilds, indicates that quite complex continental ecosystems were present close to the depositional basin. Also, the insect fossils of Val Mara site VM 12 include representatives of different trophic groups, such as detritivores, predators and herbivores. In addition, they include insects with different post-embryonic development strategies and inhabitants of both terrestrial and freshwater habitats. Interestingly, in the Val Mara site VM 12, more than one individual per taxon have been recovered (in three cases two individuals of the same taxon in the same layer), providing the opportunity to collect information on populations and age-structure (*e.g.*, in the case of *Dasyleptus triassicus* different instars of nymphs were recovered together with adults). Unlike Val Mara site D, Val Mara site VM 12 is dominated by almost intact (only a few of them are disarticulated) small to medium size insects (range: ~ 1 to 29 mm). Moreover, insects of different orders and sizes preserve fine morphological details such as setae on wings in some Thysanoptera of ~ 2 mm length, or surrounding compound eyes in Pleciofungivoridae-like Diptera. The latter preserve hexagonal ommatidia facets on the head. Within this assemblage, only a limited proportion of phosphatized individuals were found (nine of 248 individuals). This evidence suggests that Val Mara site VM 12 is representative of a complex and quite stable continental ecosystem that was located in close proximity to the depositional environment of the Upper Kalkschieferzone.

Evolutionary importance of Monte San Giorgio insect fossils

Besides the exceptional features, Monte San Giorgio insect fossils are of extreme evolutionary importance, because Triassic insects are rare globally. In fact, several fossils found at Monte San Giorgio represent the oldest or youngest occurrence of their respective lineage, thus significantly backdating the origin or postponing the extinction of some insect groups. The discovery of three *Dasyleptus triassicus* (Archaeognata, †Monura) in the Upper Kalkschieferzone of Val Mara site VM 227 (Bechly & Stockar, 2011) is a good example, because it postponed the extinction of †Monura to at least the Middle Triassic, well after what has been previously thought (i.e., end of Permian, Labandeira & Sepkoski, 1993). The finding of *D. triassicus* also in Val Mara site VM 12 and in the Upper Buntsandstein of Lower Franconia and Thuringia (Bashkuev et al., 2012) suggest that *Dasyleptus,* the only body fossil genus of †Monura, was still quite common during the Middle Triassic. In addition, a total-evidence Bayesian inference analysis recognised *D. triassicus* as the sister of a clade consisting of Machilida + Zygentoma (Montagna, 2020). Within the Kalkschieferzone, the first representative of the extant family Machilidae, *G. triassicus,* was also collected. This discovery allowed us to backdate the origin of this lineage to the Middle Triassic, approximately 200 My earlier than previously thought.

Archetingis ladinica (Hemiptera, Tingidae), discovered within the Lower Kalkschieferzone in Val Mara site D, even if poorly preserved, represents the oldest known lace bug species and pushes back the origin of the family by approximately 140 My (Golub & Popov, 2008; Popov, 1989).

The inclusion of some of the previously mentioned fossils, together with other relevant ones from Val Mara site D, as calibration nodes in a phylogenomic dating analysis led to backdating the appearance of some of the main insect lineages including crown Diptera and Heteroptera (Montagna et al., 2018), previously assumed to be of post-Permian origin.

Moreover, the discovery in Val Mara site VM 12 of a Blattodea fossil preserving peculiar features enhances the understanding of the transition from ancestral roachoids to crown cockroaches. Furthermore, the first completely preserved representative of †Permithonidae ever found also comes from this site. Until now, the members of this extinct family have been described based only on isolated wings (e.g., Tillyard, 1926; Martynov, 1933; Pinto & de Ornellas, 1980; Prokop et al., 2015).

Systematic palaeontology

Euarthropoda sensu Walossek, 1999

Insecta Linnaeus, 1758

Subclass Pterygota Lang, 1888

Infraclass Neoptera Martynov, 1923

Superorder Neuropterida Boudreaux, 1979 incerta sedis;

Family †Permithonidae Tillyard, 1922

Genus *Merithone* Montagna & Magoga, gen. nov.

Type species: *Merithone laetitiae* sp. nov. by monotypy (Fig. 3).

Code Zoobank: LSID urn:lsid:zoobank.org:act:16C0A670-1BE5-44FD-BC6C-0E10C87C3045

Etymology: *Meri-* named after Meride, the village near the locality where the fossil has been collected; the suffix *-thone* from the type genus of the family †Permithonidae, *Permithone* Tillyard, 1922. Gender feminine.

Diagnosis: the general habitus of the new taxon (new genus, new species) comprises a well-developed prothorax, shorter than meso- plus meta- thorax; the prognathous head capsule has prominent compound eyes and filiform antennae; the subequal membranous wings without pterostigma; the fore wings with broad costal area possessing several irregular veins from subcostal vein (SC) to costal margin (some distally bifurcated); the SC merging distally the radius (R), the radial sector (RS) with six primary branches; the medial anterior (MA) not coalesced with RS basally; the CUP apparently not deeply forked; and nygmata not visible prompts the ascription of the fossil to the family of †Permithonidae Tillyard, 1922.

Comparison: The new genus differs from the previously described genera based on forewing shape and features. The forewings are elongate, more than two times (~2.7) as long as wide, not broad and markedly triangular as in *Eopsychops* Martynov, 1933, *Permithone, Permopsychops* Tillyard, 1926, and *Permipsythone* Pinto & de Ornellas, 1980, not oval as in *Lodevosisyra* Prokop et al., 2015. The costal area is wider in its first half, slightly restricted at the base, but not as strongly as in *Palaemerobius* Martynov, 1928, *Permegalomus* Martynov, 1931, *Permipsythone* and *Permithonopsis* Martynov, 1933; veinlets are present and branched in the proximal part of the wing, but not reticulated as in *Permorapisma* Tillyard, 1926. The new genus is close to *Lodevothone* Prokop et al., 2015, from which it differs in the presence of branched veinlets and less than seven Radial posterior branches, and to *Permithonopsis*.

Merithone laetitiae sp. nov. Montagna & Magoga

Code Zoobank: LSID urn:lsid:zoobank.org:act:968E793A-F8F8-4B60-ADFE-E0B724A7F1EA

Etimology: *laetitiae* is derived from the prosoponym Laetitia, the daughter of the first author, to whom the species is dedicated.

Material: holotype specimen MCSN 8679, Museo Cantonale di Storia Naturale, Lugano, Switzerland.

Type horizon: upper Kalkschieferzone member of Meride Limestone Formation.

Type locality: VM12 site (45° 53′ 26″ N, 8° 56′ 49″ E), Val Mara valley near Meride (Monte San Giorgio, Switzerland).

Diagnosis: as for the genus, being the only species.

Description (Figs. 3, 4, 5). Almost complete specimen of ~6.4 mm length, preserved in dorso-lateral view. Prognathous head (0.6 mm in length) with prominent compound eyes of 0.4 mm diameter; eyes surrounded by short spines; chewing mouthpart with visible mandibles and the short maxillary palps (only the left visible); filiform antennae composed of more than 20 antennomers (2.04 mm in length) (Fig. 4). Well-developed prothorax (0.6 mm) but shorter than meso- plus metathorax; sub-rectangular, partially crushed mesothorax (length = 0.8 mm, maximum width = 0.95 mm) covered with long setae especially visible on the anterior ridge (Fig. 4). Metathorax of 0.5 mm in length and 0.67 mm of width, respectively. Forelegs visible, one almost complete (coxa, trochanter, femur of 0.8 mm, tibiae of 0.91 mm, and tarsus of 0.97 mm; Fig. 4), while only tibiae and tarsus of the other are visible. Abdomen of 1.3 mm in length partially visible.

Wings (Figs. 3, 5). Two pairs of subequal membranous wings without pterostigma and with many veins, long setae present on veins, except for the costal (C) vein, where setae are shorter and denser. Forewings

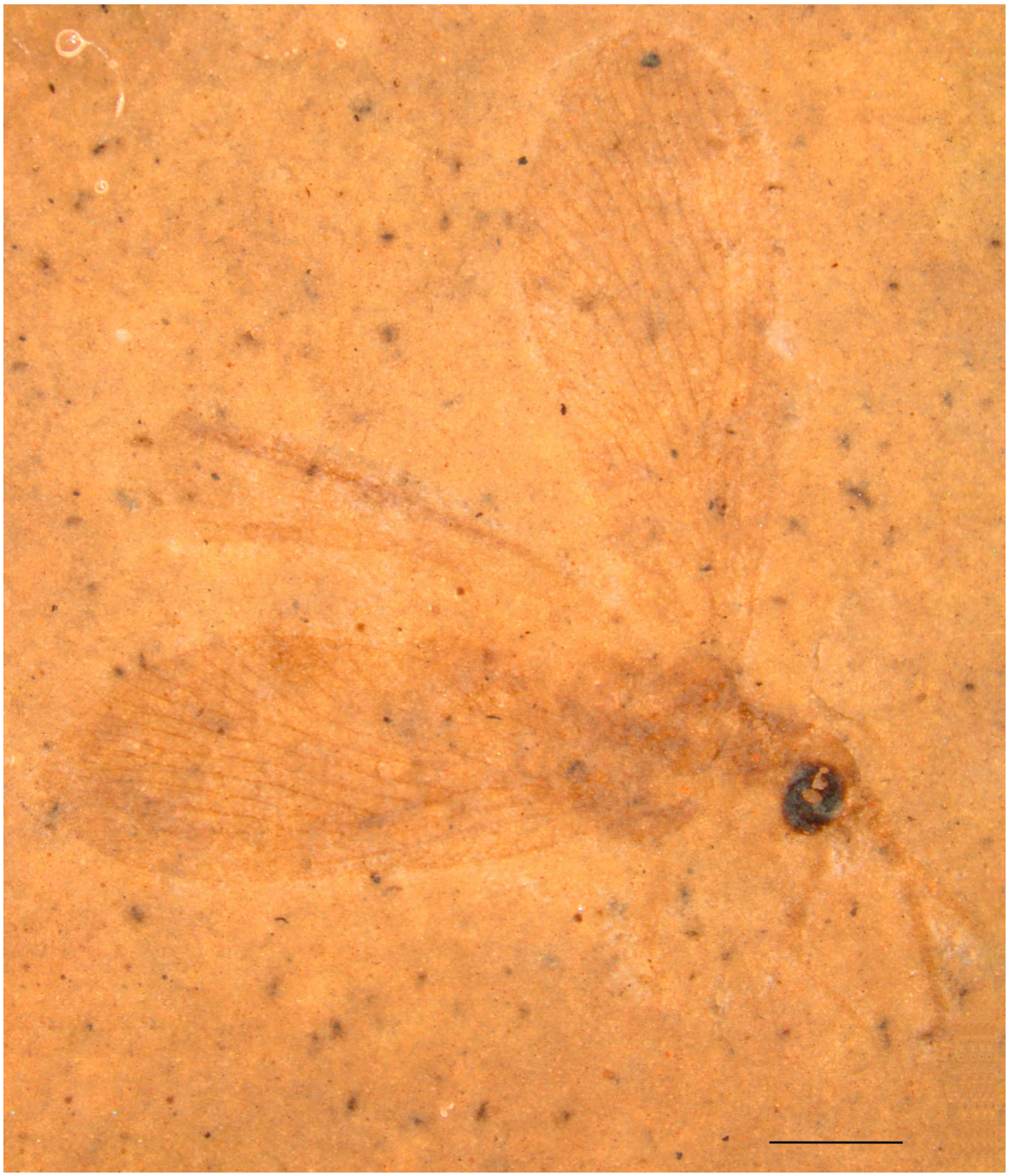

Fig. 3 *Merithone laetitiae* (†Permithonidae) gen. nov., sp. nov. Scale bar, 1 mm

elongate, ~ 2.7 times as long as wide (length: 5.1 mm; maximum width of inter radial area: 1.92 mm), with a distally rounded shape; moderately broad costal area (until its mid; maximum width 0.29 mm), then gently decreasing distally until the joining with subcostal (SC) vein, and proximally at the wing base. Costal area with numerous veinlets that, in the proximal part of the wing, are bifurcated. SC vein almost straight, terminating distally on R; few cross veins between R and RS, the latter with six primary branches. Medial (M) veins not coalesced with RS basally, the former is separated in medial anterior (MA) and medial posterior (MP). Cubital anterior 1 distally forked, cubital posterior simple. Anal veins not clearly visible.

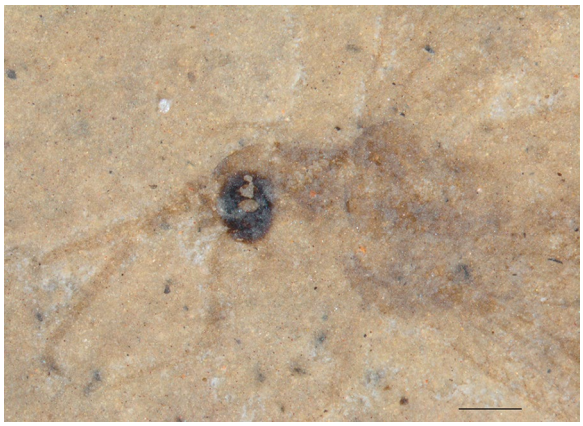

Fig. 4 *Merithone laetitiae* (†Permithonidae) gen. nov., sp. nov. head and thorax details. Scale bar, 500 µm

Hind wings are visible and subequal to forewings (Fig. 3), as demonstrated by the right hind wing almost completely overlapping the corresponding forewing, the left hind wing is crumpled, and venations are only partially visible.

Conclusions

This contribution summarises the current knowledge on the fossil insects retrieved in ~ 25 years of excavations in the Monte San Giorgio UNESCO's World Heritage Site and it includes the description of a new genus and species of †Permithonidae (*Merithone laetitiae* gen. et sp. nov.). The fossil insect fauna of Monte San Giorgio is of major importance for the understanding of insect evolutionary history. Besides the fact that insect Lagerstätten of the Triassic, a crucial period for the establishment of the modern insect fauna, are extremely rare worldwide, other main reasons are (i) the exceptional preservation of the majority of the specimens found in Monte San Giorgio main fossiliferous sites, allowing the observation of both internal and external morphological details; (ii) the discovery of new taxa, five formally described, one described in this work and another one in Montagna et al. (submitted); (iii) the phylogenetic diversity covered by these fossils; and (vi) the fact that many of the identified taxa represent the oldest or youngest occurrence for the respective insect lineages. Moreover, the large number of fossils found in limited size excavation sites, especially the Val Mara site VM 12, confirm the need for further excavation campaigns in the Monte San Giorgio that surely will lead to new significant discoveries.

Materials and methods

The holotype of *Merithone laetitiae* was collected in Val Mara valley VM 12 site near Meride (Monte San Giorgio, Switzerland). The fossil was prepared using a steel needle under a stereomicroscope (Leica M80) and high-quality pictures were acquired using the camera Olympus UC50 attached to an Olympus SZX 12 binocular. Image post-processing was performed with Adobe Photoshop CS2. The systematics of †Permithonidae as proposed by Martins et al. (2022) was adopted.

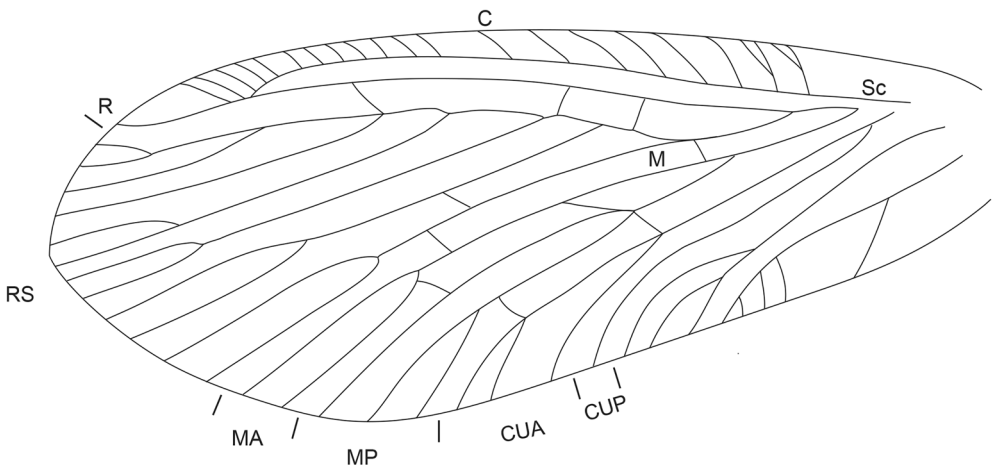

Fig. 5 *Merithone laetitiae* (†Permithonidae) gen. nov., sp. nov. forewing venation. Scale bar, 1 mm. C: Costa; Sc: Subcosta; R: Radius; M: Media; RS: Radial Sector; MA: Medial Anterior; MP: Medial Posterior; CUA: Cubital Anterior; CUP: Cubital Posterior

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Author contributions
FM collected and prepared the fossil of the new taxa. MM and GM described the new taxa and drafted the first version of the manuscript, except for the Monte San Giorgio geological setting drafted by FM. All the authors contributed to obtaining the final version of the manuscript.

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Availability of data and materials
All fossils are stored in the collections of the Museo Cantonale di Storia Naturale, Lugano (Switzerland).

Declarations

Competing interests
The authors declare that they have no conflict of interest.

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