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The contribution of the Middle Triassic fossil assemblage of Monte San Giorgio to insect evolution



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The Triassic represents a critical period for understanding the turnover of insect fauna from the Paleozoic to the Mesozoic following the end-Permian mass extinctions (EPME); however, fossil deposits from the Early-Middle Triassic are scarce. The exceptionally preserved 239 million-year-old fossil insect fauna recorded at Monte San Giorgio (Switzerland), including 248 fossils representing 15 major insect clades is presented here. Besides the exceptional features, including their small size and excellent preservation, the fossils have importance in the evolutionary history of the group. The taxonomic and ecological diversity recovered, including both freshwater (dragonflies and caddisflies) and terrestrial taxa (true bugs and wasps), demonstrates that complex environments sustained a paleocommunity dominated by monurans (thought not to have survived the EPME), midges, and beetles. Interestingly, a blattodean-like fossil bearing an external ootheca was also found, important for understanding Paleozoic roachoids to extant cockroaches' transition and the evolution of maternal brood care. Moreover, the youngest and first complete specimen of †Permithonidae and the oldest sawfly fossils were discovered. Finally, round-shaped bodies, compatible with seminal capsules or lycophyte spores, were found on the abdomens of several midge-like individuals. If these are spores, non-seed-bearing plants could have been the first entomophilous plants rather than gymnosperms, as recently supposed. Altogether, these fossils contribute substantially to understanding insect evolution and Paleozoic-Mesozoic faunal turnover.

The Triassic represents a key period for biological communities because it witnessed the rise and diversification of modern ecosystems¹ postdating the most severe extinctions of the Phanerozoic, i.e., the end-Permian Mass Extinction events (EPMEs)^{2,3}. However, it was recently hypothesized that some groups of organisms inhabiting continental ecosystems, such as plants and insects, were not dramatically affected by EPMEs as previously thought and likely experienced faunal turnover rather than mass extinction^{4–6}. This period was particularly crucial for insect evolution, witnessing the disappearance of some Paleozoic lineages, such as the Palaeodyctioptera and Megasecoptera⁷, and the emergence of representatives of many extant orders^{8,9}. It is also worth noting the radiation of holometabolous insects^{5,10,11}, as well as the evolution of new kinds of interactions between plants and insects that strongly affected the structure of the terrestrial food webs. Of particular interest is the appearance of pollination of Cycadales, Gnetales, and Bennettitales¹². Altogether, these evolutionary events, possibly promoted by changes in floral assemblages¹³,

led to the turnover from the Paleozoic to the modern insect fauna during the Early-Middle Triassic. However, the Triassic history of insects, even considering the new insect records of Ladinian and Carnian deposits from China¹¹, remains enigmatic, because of the rarity of Early-Middle Triassic fossils. This scarcity of fossils is possibly due to the limited number of fossil deposits for these epochs. Indeed, only eight main insect Lagerstätten are currently known and few of these are recognized as konzentrat Lagerstätten⁶. A further potential explanation for the paucity of Triassic fossils is the global insect community depletion caused by the cascading effects following the EPMEs e.g.^{14,15}.

Here, an exceptionally preserved and diversified Middle Triassic (Ladinian) insect fauna consisting of 248 specimens collected in the newly discovered insect konzentrat Lagerstätte of Monte San Giorgio (VM12 site, Val Mara, upper Kalkschieferzone of the Meride Limestone¹⁶) is described. At this locality, there are fossil representatives of fifteen major insect lineages, inhabiting both terrestrial and freshwater ecosystems, whose

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exceptional preservation allows us to gain new and important information on the ecology and evolution of Triassic insects.

Results

The insect fossil assemblage discovered at the Monte San Giorgio

A total of 248 insect fossils were collected from three small excavations (total surface area = 9 m²; total stratigraphic thickness = ~ 150 cm) from the upper Kalkschieferzone (~ 239 Mya¹⁷) in the Val Mara Valley, Monte San Giorgio (MSG), Meride (Switzerland; Fig. 1). The insect fossils were assigned to 13 major lineages (Table S1; Figs. 2–4): †Monura (74 individuals), Odonata (1),

Blattodea (1), Thysanoptera (29), Hemiptera (5), Psocodea (1), Hymenoptera (2), Neuropterida (7, one of which assigned to †Permithonidae), Coleoptera (37), Trichoptera (3), Amphiesmenoptera (2), Mecoptera (1), Diptera (56). Moreover, 29 individuals were assigned to *incertae sedis* as their taxonomic assignment to a specific group cannot be stated with certainty due to partial preservation.

Main insect lineages discovered in the Monte San Giorgio upper Kalkschieferzone Lagerstätte

†Monura. 74 specimens were found in ventral and lateral position and assigned to the jumping bristletail *Dasyleptus triassicus* (Archaeognatha, †Monura), based on the presence of large maxillary palps, short antennae but longer than the head, abdominal *styli* and terminal filament longer than the abdomen. The individual size, ranging from ~ 1 to ~ 29 mm in length (head to terminal filament), indicates different developmental stages. Some individuals are almost complete (MCSN 8687, 8688; Fig. 2A, B), while others present only the terminal filament plus the last sternites.

Odonata. An elongate naiad of ~ 10.5 mm in length (from head to abdominal apex), was assigned to Odonata (MCSN 8666; Fig. 2C). The specimen, preserved in dorsal view, is characterized by a laterally and strongly expanded head of ~ 2.5 mm in width and ~ 1.2 mm in length (width-length ratio of 2.1), with wide compound eyes and a cervical region strongly constricted (Fig. 2C). The mouthparts are preserved, and a raptorial mask protruding anteriorly from the head capsule is visible, including developed maxillary palps (Fig. S1A, B). Antennae consist of six segments. On the thorax, wing pads are visible (extending to the middle of the abdomen) and present grooves that can be interpreted as wing tracheation (Fig. S1C); six robust partially preserved legs, some with 3-segmented tarsi, are also visible. The abdomen preserves three posterior abdominal processes composing the anal pyramid: a central, wide and possibly long epiproct (truncated abruptly at the base but likely a *postmortem* effect), and two lateral paraprocts that retain setae (Fig. S1D).

Blattodea. One complete specimen (MCSN 8667; Figs. 2D, E, S2) of ~ 11 mm in length from the clypeus to the apex of the ovipositor (excluding the long filiform antennae) and attributed to Dictyoptera *sensu stricto* (*sensu* Béthoux et al.¹⁸) due to the presence of well-developed euplantulae, an arcuate cubitus in the forewings, and the presence of an external and mobile short ootheca (~ 1.5 mm of length, ~ 0.65 mm of width) apparently bearing less than 20 eggs and protruding from the abdomen (Figs. 2D, E, S2B). The specimen preserves cursorial legs, cone-shaped coxae, spines and hooks on femurs and tibiae. Both forewings and hindwings, with colored black-white pattern, are preserved. Long and well-developed valvules leading to a sword-shaped ovipositor are visible and the basal part of cerci as well (Figs. 2D, S2B). The sub-genital plate is not visible, but the poor preservation of this area does not allow us to confirm its presence. All these features suggest that the specimen MCSN 8667 probably belongs to Blattodea.

Thysanoptera. Twenty-nine out of the 248 collected fossils were assigned to Thysanoptera due to the presence of narrow wings fringed with long cilia (Figs. 2F, S3). Most of the specimens are well-preserved adults (mainly in dorsal view, except specimen MCSN 8689 in lateral view, Fig. S4A), having length ranging from ~ 1.6 mm to ~ 2.4 mm. Eyes are relatively large, visible on specimen MCSN 8670 (Fig. S4B, C) and antennae have nine antennomeres (MCSN 8671, 8672, Fig. S5). Forewings are broad, with a maximum length of ~ 1.1 mm and width of ~ 0.35 mm. The forewings are similar to *Triassothrips* or *Kazachothrips* in shape and veins M2 and M1, while other features such as the straight longitudinal vein R and the length of Rs are typical of *Karataothrips*. However, forewings are shorter than those of *Triassothrips* and not reaching the anterior margin of the penultimate abdominal tergite. Moreover, the MSG thrips also have margins of wings with cilia on the distal part of longitudinal veins (clearly visible on MCSN 8673, Fig. S3A), apparently absent both in *Triassothrips* and *Karataothrips*. The features observed in MSG thrips suggest that they likely belong to a new genus.

Hemiptera. A total of five specimens (~ 1.3 mm to ~ 2.6 mm in length) were assigned to Heteroptera (possibly Cimicomorpha) based on general

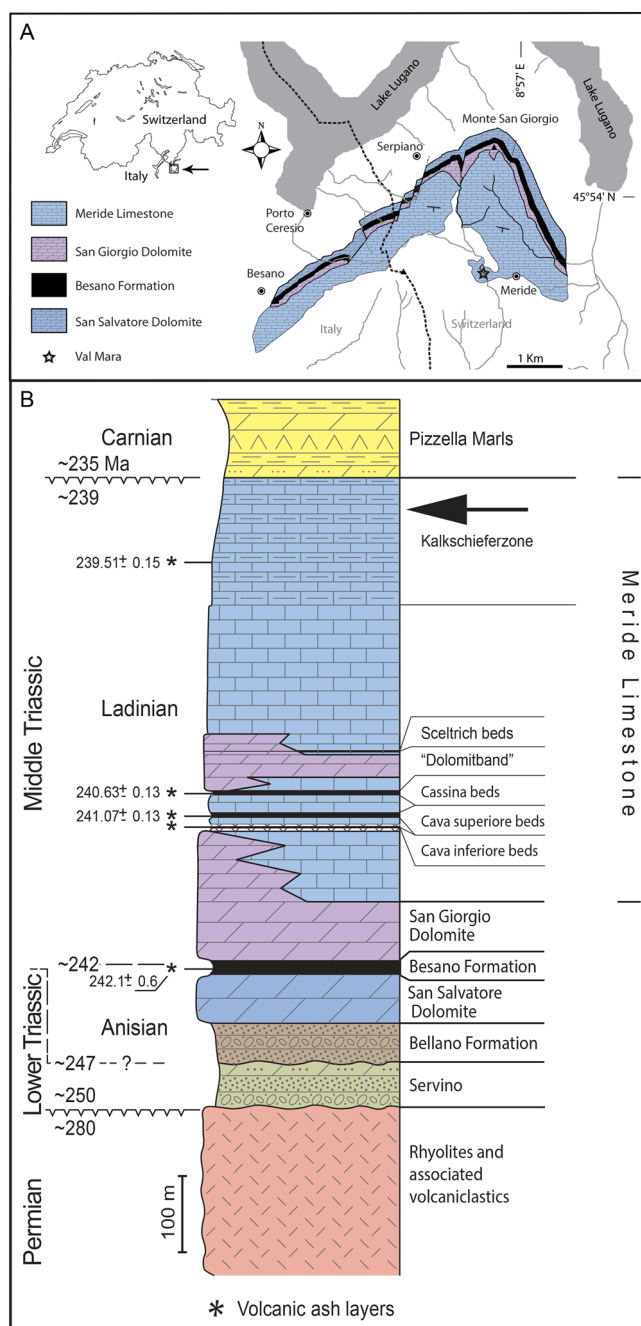


Fig. 1 | Location of the Monte San Giorgio (Italy-Switzerland) UNESCO World Heritage and stratigraphic section of the Middle Triassic sediments. A Simplified map of the Monte San Giorgio showing the Middle Triassic carbonate succession and the location of Val Mara (indicated by a star) where VM 12 site occurs. **B** Stratigraphic section of the Middle Triassic sediments in Monte San Giorgio, the position of VM 12 strata where the insect fossils were collected is indicated by the black arrow.

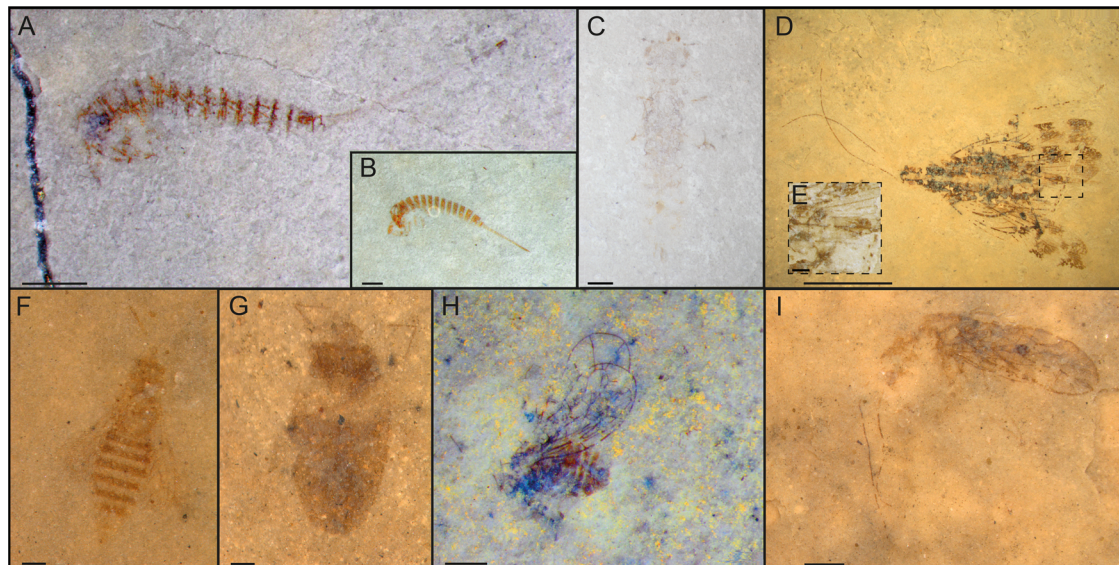


Fig. 2 | Representatives of ametabolous and hemimetabolous insects.

A *Dasypleptus triassicus* (†Monura), MCSN 8688. **B** *Dasypleptus triassicus* (†Monura), MCSN 8687. **C** Odonatan naiaid, MCSN 8666. **D** Blattodean, MCSN 8667. **E** Enlargement of the external ootheca of MCSN 8667. **F** Thysanoptera, MCSN 8668.

G Hemiptera, MCSN 8677. **H** *Incerta sedis*, MCSN 8689, possibly Hemiptera of the superfamily Protopsyllidoidea. **I** Psocodea, MCSN 8690. Scale bars: **A**, **C**, 1 mm; **B**, **E**, **I**, 500 µm; **D**, 5 mm; **F**–**H**, 200 µm.

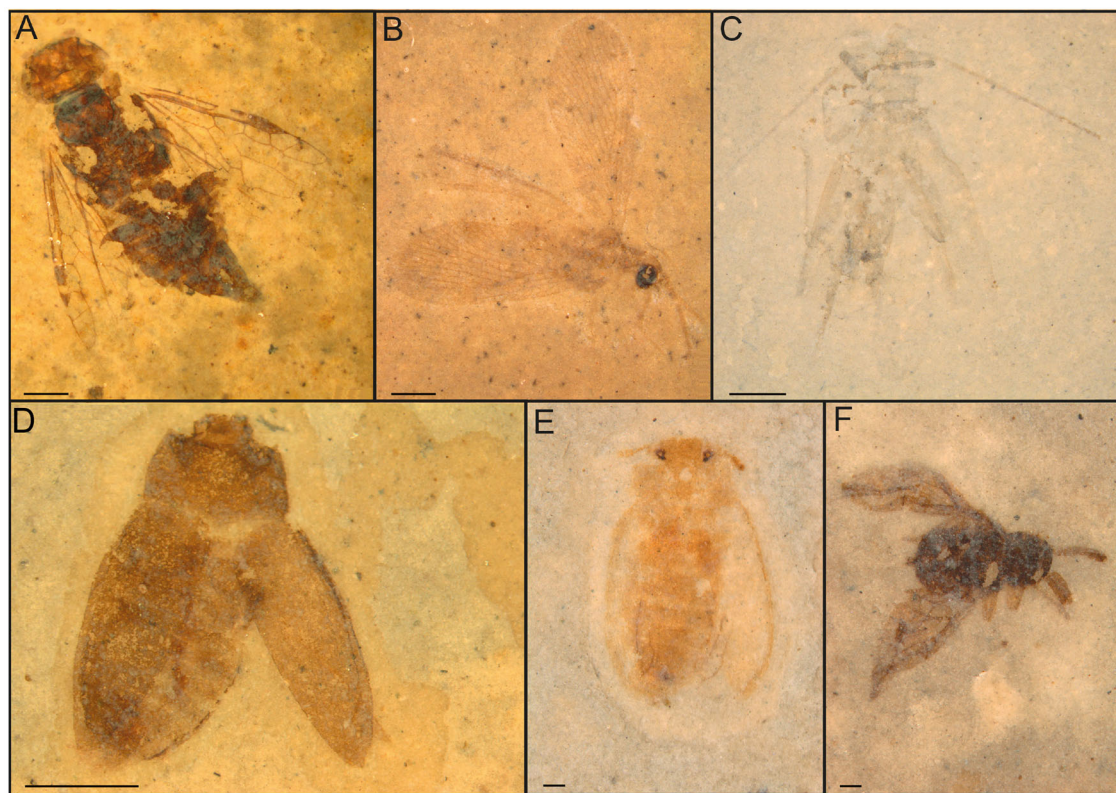


Fig. 3 | Representatives of holometabolous insects. **A** *Magnicapitixyela dilettae* (Hymenoptera, Xyelidae), MCSN 8678. **B** *Merithone laetitiae* (Neuropterida, †Permithonidae), MCSN 8679 (19). Coleoptera: MCSN 8691, Archostemata

(C); MCSN 8692, Archostemata (D); MCSN 8681, Adephaga (E); MCSN 8693, Polyphaga (F). Scale bars: **A**–**D**, 1 mm; **E**, **F** 200 µm.

habitus, four-segmented antennae (MCSN 8674, 8675; Fig. S6A, B), hemielytra presence (MCSN 8677, 8676, Figs. 2G, S6C), and pronotal shield (Fig. 2G). The specimen MCSN 8689 (Fig. 2H), currently considered as *incertae sedis*, possibly belongs to Protopsyllidoidea (Sternorrhyncha) based on wing shape and venations.

Psocodea. Only one specimen was assigned to this group based on the general habitus and wing venation pattern (MCSN 8690; Fig. 2I).

Hymenoptera. Two almost complete and well-preserved specimens (one male and one female) were assigned to Hymenoptera (MCSN 8678, 8683; Figs. 3A, S7, S8) due to the simple wing venation pattern and hindwings

smaller than forewings, which are connected to the latter by hamuli, and more specifically to the Symphyta lineage due to the abdomen's broad attachment to the thorax. These specimens belong to family Xyelidae based on radial sector (RS) two-branched in forewings. The presence of a narrow costal space, costal vein (C) separated from pterostigma and thickened toward apex reaching the radius (R) vein but not touching it, suggests they may belong to the extinct subfamily †Madygellinae. However, MSG sawfly differs from the members of this group due to the presence of a robust subcostal vein (Sc).

Systematic palaeontology. Euarthropoda sensu Walossek, 1999; Insecta Linnaeus, 1758; Order Hymenoptera Linné 1758; Suborder Symphyta Gerstaecker, 1867; Family Xyelidae Newman, 1834; Genus *Magnicapitixyela* Montagna M. & Magoga G., gen. n.

Type species: *Magnicapitixyela dilettae* sp. n. by present designation.

Code Zoobank: LSID urn:lsid:zoobank.org:act:62299AF2-5601-4192-8BD9-D7BC38D447A3.

Etymology: *Magni-* from the Latin *magnus* meaning big, *capiti-* from the Latin *caput* meaning head and *-xyela* from Xyelidae, the family to which *Magnicapitixyela* is ascribed. Meaning: *Xyela* with a big head.

Diagnosis: Small sawfly, forewing with narrow costal space, C thickened towards apex, reaching R (but not touching), sclerotized pterostigma, thick subcosta (SC), joining only C, R thicker than SC and sinuous; RS1 + 2 present; RS + M is ~ 1.3 times as long as 1-RS. M + cubital anterior (CuA) slightly concave until the split between M and CuA. 2m-cu straight while 3r-m sinuous. Anterior margin of cell 1r almost equal to 2r in length; cell 1-mcu ~ 3 times as long as high, distally dilated.

Comparison: The new genus differs from other Triassic genera in the fully sclerotized pterostigma (not as in *Archexyela* Riek, 1955; *Lithoxyela* Rasnitsyn, 1969; *Sirecomima* Rasnitsyn, 1969); forewing slender, more than twice as long as wide (broad in *Euryxyela* Rasnitsyn, 1964, broad and triangular in *Ferganoxyela* Rasnitsyn, 1969); costal area not narrow as in *Lithoxyela* Rasnitsyn, 1969, *Madygenius* Rasnitsyn, 1969, *Xiphoxyela* Rasnitsyn, 1969 and *Xyelinus* Rasnitsyn, 1964; cell 1r longer than 2r (almost of the same length in *Leioxyela* Rasnitsyn, 1969), presence of cells 3r and 4r (absent in *Madygella* Rasnitsyn, 1969), cell 3r wide (reduced in *Triassoxyela* Rasnitsyn, 1964). *Magnicapitixyela* gen. n. is close to *Madygella* Rasnitsyn, 1969 due to the well-sclerotized pterostigma, well developed and distinct SC, basal section of RS shorter than RS + M.

Magnicapitixyela dilettae sp. n. Montagna M. & Magoga G.

Code Zoobank: LSID urn:lsid:zoobank.org:act:0C78D2B1-A392-49A6-8C92-FE606E044476.

Etymology: Specific epithet *dilettae* is derived from the prosoponym of the first author daughter Diletta, to whom the species is dedicated.

Material: *M. dilettae*, holotype MCSN 8678, an almost complete male specimen (Figs. 3A, S7); and paratype MCSN 8683, a partially preserved phosphatized female specimen (Fig. S8); both fossils in dorsal view.

Type horizon: Upper Kalkschieferzone member of Meride Limestone Formation (transition interval to Archelaus and Regoledanus Ammonoid Zones; upper Ladinian).

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

Repository: Museo cantonale di storia naturale, Lugano, Switzerland.

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

Description (Figs. 3A, S7, S8). Small sawfly with a body length of 7.8 mm (♂) and of 8.1 mm (♀), including the ovipositor. Abdomen width (at III urite level) = 2.6 mm. Head capsule (frons apex–post occipital sulcus) = 1.3 mm (♂) and 1 mm (♀), gena–gena margins = 2 mm (♂) and 1.7 mm (♀), eyes very large and three ocelli visible on the holotype (diameter of 0.26 mm) (Fig. S8B). Antennae poorly preserved, visible only the scape. Head capsule almost of the same width as the thorax, mesoscutum well-developed. Forewing almost totally preserved in the holotype (only partially visible on the paratype), with a length of ~ 5.3 mm and a width (at distal upper apex of pterostigma and 2cu distal lower apex) of 1.74 mm, wing length/width ratio = 3.05, tegula visible on the left forewing (Fig. S7). Pterostigma completely sclerotized, SC developed over the entire length, joining C approximately at RS base (Fig. S7). R sinuous, slightly dilated at

RS base. 1-RS and RS + M are slightly longer than 1-M (~ 1.4 times) and 1-RS (~ 1.3 times), respectively. Angle between 1-RS and RS-M of forewings of 146°. M + CuA slightly concave until the split between M and CuA. 1 A straight. Presence of cells 3r and 4r; cell 1 mcu ~ 3 times as long as high, distally dilated; cell 2 rm wide, ~ 3 times as long as width. Hind wing only partially preserved. Legs partially preserved, mostly only femur and tibia are preserved; tarsus and tarsal claws visible on the paratype (Fig. S8). Abdomen almost completely preserved, with ten visible segments. The paratype preserves the ovipositor with the 3rd valvulae of 1.3 mm in length and a maximum width of 0.35 mm, transversal ornamentations are visible (Fig. S8C).

Neuropterida. Seven almost complete fossils (length ranging from ~ 2.4 mm to ~ 6.5 mm) were assigned to Neuropterida based on shape and venation pattern of wings; some specimens possess nygmata. Six specimens resemble Raphidioptera, while one almost complete specimen was assigned to the extinct family †Permithonidae Tillyard, 1922 (MCSN 8679; Fig. 3B) and recently described as a new genus and species, *Merithone laetitiae* Montagna and Magoga, 2024¹⁹.

Coleoptera. Thirty-seven specimens were found in the MSG assemblage, most of them completely preserved, and assigned to Coleoptera based on highly sclerotized exoskeleton and forewings transformed into sclerotized elytra. The assemblage includes representatives of three out of the four beetle suborders, namely Archostemata (Cupedidae *incertae sedis* MCSN 8691, 8692; Fig. 3C, D), Adephaga (MCSN 8681; Fig. 3E) and Polyphaga (MCSN 8693; Fig. 3F). The fossils consist of small to medium size specimens (~ 1.3 mm to ~ 6.9 mm in length) characterized by terrestrial and aquatic habitus. Natatorial hind legs are visible in the specimen MCSN 8681 (Fig. 3E).

Amphiesmenoptera. A ~ 3.6 mm almost complete insect preserved in dorsal view (MCSN 8701; Fig. S9A). Head with hair on the front, rather complete filiform antennae and eyes partially visible. Both fore and hind wings are visible (left wings superposed), presenting hairs along the margins, nygmata not visible. Forewings with 3-branched M vein, as in Lepidoptera; the separation between M1 and M2 veins forms an angle greater than 45°, which precludes its assignment to Trichoptera, but in the meantime not greater than 60° as in Lepidoptera. Legs are partially visible on the right side. A second almost complete fossil in ventral view (MCSN 8702, a male; Fig. S9B) may belong to the same morphospecies because of the similar habitus and size (~ 2.8 mm). However, in this case, the 3-branched M vein in the forewing is not visible due to the poor preservation of the area. On the head, compound eyes and filiform antennae are visible, as well as, elongate structures compatible with laciniae departing from the mouthpart region. Abdomen terminal appendages visible.

Mecoptera. A small (~ 4.2 mm in length), almost complete, insect preserved in lateral view was attributed to Mecoptera due to the presence of the genital bulb folded underneath the distal part of the abdomen, likely a *postmortem* position acquired in the depositional environment (MCSN 8699; Figs. 4A, S10). The head with well-developed compound eyes, ocellus, and an elongate rostrum with maxillary palps; bristles are present on the vertex (Fig. S10A). Antennae are filiform and composed of at least by 26 segments. Legs are partially visible. Two pairs of subequal wings with pterostigma and setae on the venations are present. CUA of forewings is not visible due to the poor preservation of the area and to the partial overlap of fore- and hindwings.

Diptera. A total of 56 fossils (54 adults and two pupae), with different degrees of preservation, were attributed to Diptera (MCSN 8686, 8673–8676, 8694–8698; Figs. 4B–D, 5A, S11). Adults (length from ~ 1.5 mm to 4.9 mm) possess hind wings reduced to halteres and one Cu vein on the forewings. Moreover, the presence of filiform antennae with more than ten segments and CuA veins not coalesced with 1 A (when visible) prompted their ascription to the Nematocera clade. The almost complete exarate pupae (MCSN 8698, ~ 4.1 mm in length, ~ 1.5 mm width, Fig. 4D; MCSN 8686, ~ 5.7 mm in length, ~ 1.4 mm width, Fig. S11A) can be assigned to Nematocera *incertae sedis* as well. These specimens preserve three pairs of legs, antennae, and respiratory horns on the head capsule. On the distal part



Fig. 4 | Representatives of holometabolous insects (Antliophora). A Mecoptera, MCSN 8699. Diptera: MCSN 8694, adult (B); MCSN 8695, adult male (C); MCSN 8698, pupa (D). Scale bars: A–B, 500 μ m; C, D, 1 mm.

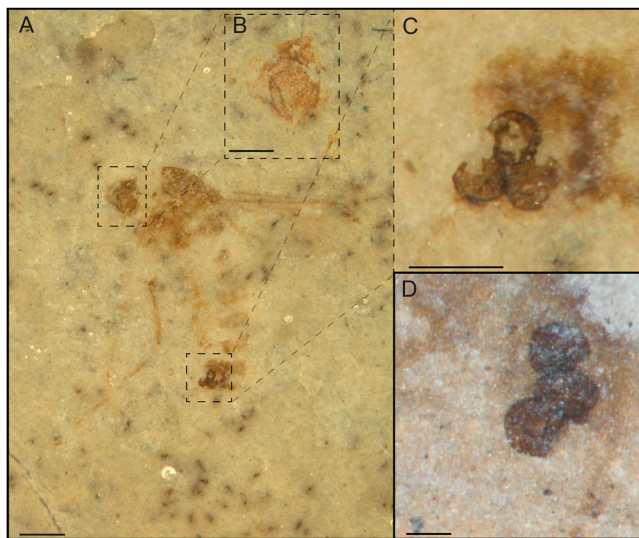


Fig. 5 | Diptera preserving peculiar features. A MCSN 8696, adult preserving the hexagonal facets of compound eyes and three round-shaped bodies at the end of the abdomen. B MCSN 8696, enlargement of the hexagonal facets of compound eyes. C MCSN 8696, enlargement of the three round-shaped bodies present externally on the abdomen, with visible ornamentations. D MCSN 8697, three round-shaped bodies present externally on the abdomen, with visible ornamentations. Scale bars: A, 500 μ m; B, C, 200 μ m; D, 100 μ m.

of the specimen MCSN 8686, the abdomen preserves ovoidal structures attributable to seminal capsules (Fig. 5A).

Among these dipteran fossils, six out of 56 are phosphatized but no soft tissues or inner organs are recognizable (Fig. S11B–E). Some adults are complete and well preserved; setae are visible on legs, wings, and at the margin of compound eyes; in some cases, the outlines of the hexagonal facets within compound eyes are visible (Fig. 5A, B). The specimen MCSN 8680 presents a prolonged labium and maxillary palps (Fig. S6). Interestingly, twelve Plecofungivoridae-like fossils possess round-shaped bodies adhering to the distal part of their abdomens (Fig. 5A). These bodies appear to be external to the abdomen, which appears intact and their texture differs from the thin cuticula of the urites. On each insect are present two to four round-shaped units (each with a diameter of ~ 100 – 130 μ m) with visible ornamentation (Fig. 5C, D). The shape of these enigmatic bodies is compatible with the one of seminal capsules as well as lycophyte spores of the genus *Reticulatisporites* (Lycopodiopsida), even if based on literature the size of the latter is ~ 65 μ m (19). The association of these enigmatic round-shaped bodies with the insect abdomen (mean = 2.83 for the round-shaped units) is not random, indeed their abundance on insect bodies significantly differs

from the one of those dispersed into the fossil matrices (mean = 0.09 round-shaped units) (Wilcoxon rank sum test results: $W = 0$, p -value < 0.001).

Discussion

The knowledge of the Middle Triassic insect fauna of Monte San Giorgio (MSG), previously consisting of 25 fossils belonging to eight different major insect lineages^{20–25}, has increased significantly with this study, which revealed the high taxonomic diversity and community complexity. After the discovery of the 248 fossils in the Val Mara VM12 site, MSG insect fauna comprises a total of 273 specimens representative of 19 major insect lineages, and include taxa considered rare in Triassic deposits such as monurans, thrips, true bugs, and flies. Moreover, in VM12 both terrestrial and freshwater taxa were found, including representatives of ametabolous, hemimetabolous and holometabolous lineages with a variety of ecologies (e.g., detritivores, predators and herbivores; Fig. 6A). The fossil community was dominated by holometabolous insects (86.3%), mainly Diptera ($\sim 23\%$) and Coleoptera ($\sim 15\%$). Ametabolous insects, represented by †Monura (29.8%), and hemimetabolous lineages (16.9%) with Odonata, Blattodea, Thysanoptera, Hemiptera and Psocodea as representative groups were less abundant. The taxonomic and ecological richness retrieved allows us to hypothesize that a diversified continental landscape able to support a complex insect community, characterized by both terrestrial and freshwater habitats, was present near the depositional environment. The existence of such a complex community at MSG is supported by the recovery of specimens articulated and well-preserved (e.g., thrips with dense fringes of hairs on wings, dipterans with hexagonal facets in compound eyes; Figs. 2F, 5B), suggesting a short transport distance from the site of insect death to the depositional site.

Interestingly, the insect fossil community of the Val Mara VM12 deposit is characterized by small-sized individuals (~ 1 mm to ~ 5 mm in length) such as thrips, beetles and flies, which only rarely possess phosphatized tissues. The insect fossil community from the upper Kalkschieferzone differs in size from that of the slightly older lower Kalkschieferzone (239.51 Mya¹⁷). Specifically, the former is dominated by small to medium size insects while the second consists exclusively of medium to extremely large size fossils (e.g., the giant jumping bristletails *Gigamachilis triassicus* measuring ~ 80 mm²³) and the holometabolous larva of ~ 40 mm in length⁵).

Another peculiar feature of VM12 site is the concentration of fossils. Although the total abundance of specimens discovered in the Kalkschieferzone of the Meride Limestone is lower than that found in the most important Triassic insects' fossiliferous sites (e.g., Grès à Voltzia of France, Madygen Formation of Kyrgyzstan, Molteno Formation of South Africa, and the Mine Group of Japan; Fig. 6B), it is notable that the 248 fossils were extracted from a ~ 9 m² excavation surface. This indicates a high probability of insect detection at this site, as further demonstrated by the discovery of two insects on the same ~ 30 cm² layer (Fig. S12). Based on these observations, the status of insect Konzentrat Lagerstätte can be assigned to the MSG

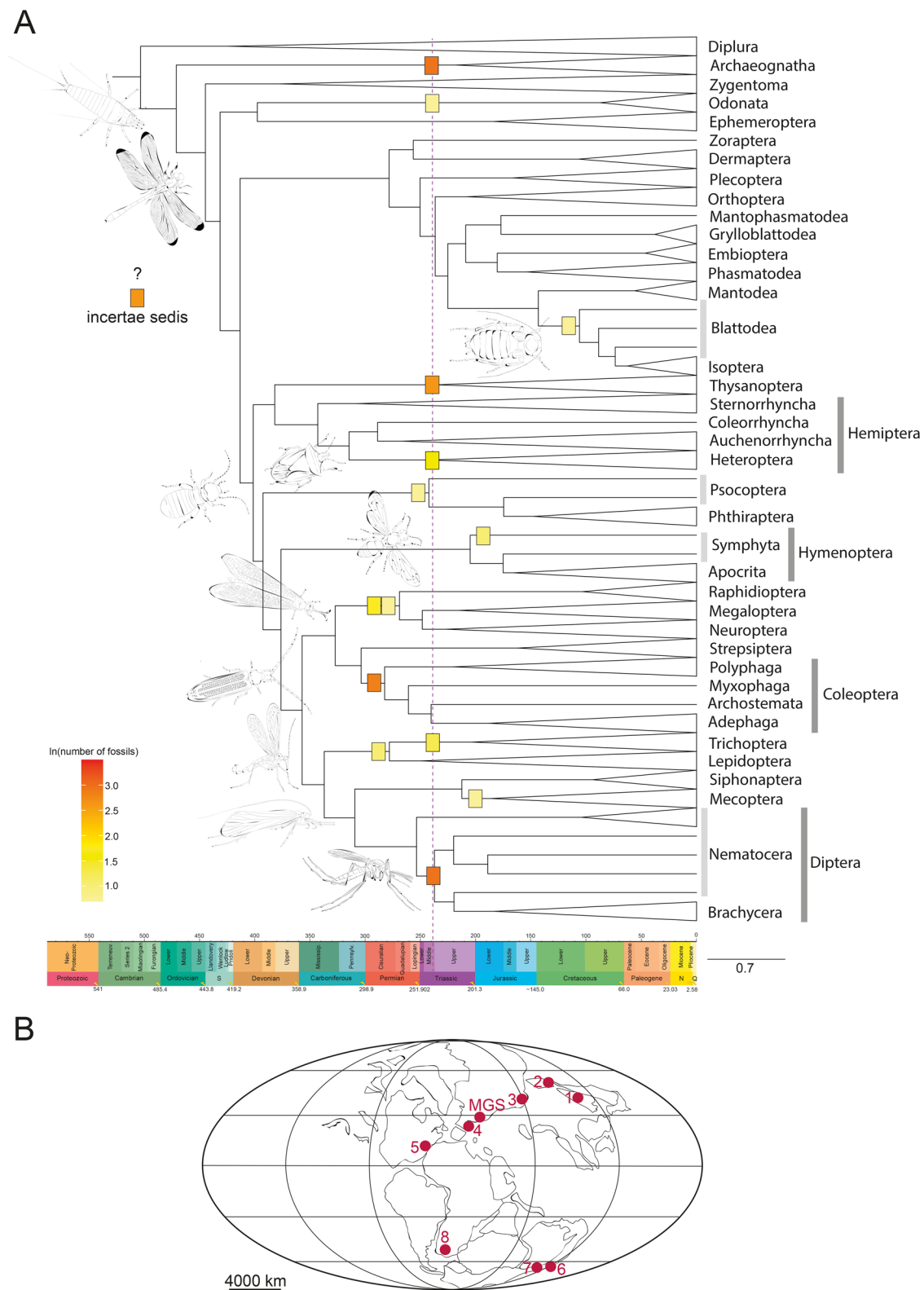


Fig. 6 | Abundance of fossils per insect lineage found at VM12 site and location of the main Middle Triassic insect deposits. A Time-calibrated phylogenetic tree of insect evolutionary relationships from Montagna et al. (5) where the abundance of insects collected at VM12 per lineage, expressed as the natural logarithm of the number of individuals, is reported; **(B)**. Location of main Middle Triassic fossil insect deposits as in Zheng et al. (11) with the addition of Monte San Giorgio. (1)

Tongchuan, China (Ladinian); (2) Karamay, China (Carnian); (3) Madygen, Kyrgyzstan (Ladinian-Carnian); (4) Vosges, France (early Anisian); (5) Solite, USA (late Carnian); (6) Ipswich, Australia (Carnian); (7) Brookvale, Australia (Anisian); (8) Molteno, South Africa (Carnian); (MSG) Monte San Giorgio, Switzerland (Ladinian). Giulia Magoga drew insect silhouettes.

deposit (according to Schachat and Labandeira (6)), previously well known only for its vertebrate assemblage e.g.²⁶.

Besides the exceptional concentration, preservation and diversity of fossil insects in the MSG deposit (Figs. 2–5, S1–S12), some of the discovered taxa have major implications for the understanding of insect evolution.

†Monura. The discovery at the MSG deposit of several *Dasyleptus triassicus* individuals at different ontogenetic stages (from first instar nymph to adult), further disproves the hypothesis that the *Dasyleptus* fossils recovered from the Carboniferous to the Middle Triassic are immature instars of Machiloidea. Our observation supports Rinehart and colleagues' conclusions regarding *Dasyleptus brongniarti* from the Middle Permian²⁷. Moreover, the *Dasyleptus* individuals discovered in the Val Mara VM12 site together with those found in the other deposits, such as the lower Kalkschieferzone of MSG and the Upper Buntsandstein of Lower Franconia and Thuringia^{21,28}, demonstrate that *Dasyleptus* was still common during the Middle Triassic and coexisted with representatives of extant Machilidae (*G. triassicus*)²³. This observation has led to the conclusion that global-scale events (e.g., the Carnian Pluvial Episode of the Late Triassic, ~234 to ~232 Mya) other than those occurred at the end of the Permian led to significant changes in global climate and biota composition^{29,30}, promoting the extinction of †Monura and possibly of other Paleozoic insect lineages.

Odonata. The naiad is one of the few odonatan fossils so far known for Triassic at this developmental stage^{31,32}. This odonatan naiad, which has a labial mask but still retains developed maxillary palps (Fig. S1B), might represent a transition towards the evolution of the currently typical odonatan labium specializations that occurred during the Carboniferous³³. Alternatively, this fossil presents a plesiomorphic state of the character. The naiad does not possess broad leaf-like caudal gills of the Samarura-type, such as those preserved in other Triassic representatives of the group^{31,32}, and thus likely had rectal respiration. The appendicular processes comprising the anal pyramid, interpreted as epiproct and paraprocts, resemble those observed in extant anisopterans, supporting the attribution of this fossil to anisopterans or a stem anisopteroid lineage. This fossil may thus represent the oldest anisopteran known so far, extending the fossil record of the group by approximately 40 My³⁴, in agreement with recent divergence time estimations obtained using transcriptome-based 2,980 protein-coding genes³⁵. Nevertheless, due to fossil preservation and the difficulties in the interpretation of the anal pyramid, this last conclusion cannot be stated with certainty.

Blattodea. Dictyoptera *sensu stricto*, including Mantodea and Blattodea, is a successful group of insects that was already abundant in the Late Carboniferous forests. The specimen discovered at MSG has an elongated ovipositor and an external short ootheca bearing less than 20 eggs (Figs. 2D, E, S2B). Notably, the last structure is recognized as the most important autapomorphy of extant dictyopterans^{36,37}. This fossil represents an exceptional finding since only a few blattodean fossils possessing ootheca have been described so far^{8,38–41}. Moreover, the discovery of a blattodean-like individual with an external ootheca in a ~239 million-year-old fossil deposit sheds light on the transition from ancestral roachoids, characterized by long and slender ovipositor valves allowing the laying of single eggs into the substrate, to extant cockroaches, characterized by a drastic reduction in length of the ovipositor valves until they are concealed by the sub-genital plate. So far it has been thought that this adaptation allowed the internal production of the ootheca, its transport on the abdomen and the egg protection, leading thus to the evolution of maternal care in cockroaches³⁹. Since the fossil here presented has both sword-shaped elongate ovipositor valves, not as long as those of Carboniferous roachoids, and external short ootheca (Figs. 2D, E, S2B), three conclusions of importance for clarifying some aspects of dictyopteran evolution can be drawn: *i.* the appearance of the ootheca in cockroaches, and thus in general of maternal brood care in insects, dates back at least to the Middle Triassic, and not to Early Cretaceous^{39,41–43} or Jurassic⁴⁴ as previously thought; *ii.* the ootheca has evolved as a structure to protect and bear only a few eggs; and *iii.* the reduction in length of the ovipositor valves was not a prerequisite to producing the ootheca. The latter statement implies that the dramatic ovipositor reduction occurred after the ability to deposit eggs within this

coriaceous structure was gained. In general, this fossil also suggests that the reduction of the ovipositor valves likely occurred independently in the Mantodea and Blattodea lineages. Furthermore, this finding aligns with recent research indicating the independent evolution of ootheca structural proteins, such as glycine-rich protein and fibroins, in Blattodea and Mantodea⁴⁵. In this regard, end-Permian and Early-Middle Triassic paleoenvironment fluctuations might have represented the driving forces for ootheca evolution as a strategy to protect the progeny.

Thysanoptera. Notably, within the MSG fossil assemblage are present 29 well-preserved thrips (Figs. 2F, S3–S5), insects considered quite rare in Triassic deposits⁴⁶. The ~239 My old fossils of the present work represent the oldest known thrips; members of this clade were found only from the Upper Triassic of North Carolina (USA), and Kazakhstan^{46,47} (~221 Mya). Despite the similarity with *Triassothrips* and *Kazachothrips*, these fossils cannot be assigned to a described genus since they present fringe cilia in the distal part of longitudinal veins (considered a derived character).

Hemiptera. The discovery of five true bug fossils of four different taxa of Heteroptera (Figs. 2G, H, S6), together with the previously described lace bugs from the lower Kalkschieferzone²⁴, and the other true bug fossils from the Triassic Tongchuan Formation in China, Grès à Voltzia Formation in France, and Cow Branch Formation in North Carolina^{11,48,49}, indicate that heteropteran lineages, including those belonging to the Cimicomorpha, were already well differentiated during the Middle Triassic. This finding is also in accordance with a previously published molecular dating analysis⁵⁰.

Hymenoptera. So far, the earliest sawfly fossils date back to ~235 Mya from the Madygen Formation (Kyrgyzstan)^{51–53}. Other sawflies were recovered from the Triassic deposits of Mount Crosby in Australia^{54,55}, Molteno Formation in South Africa⁵⁶, Potrerillos Formation in Argentina⁵⁷, and Momonoki Formation in Japan⁵⁸. *Magnicapitixyela dilettae* gen. sp. n. (Figs. 3A, S7, S8) described here represents the oldest sawfly and the first from Europe ever found, confirming the broad distribution pattern across Pangea of this group of insects. Notably, *M. dilettae* differs from members of the subfamily †Madygellinae in wing venations such as the presence of a robust subcosta, suggesting it is new extinct hymenopterian lineage. Based on the wing venation, the new genus can be considered close to the genus *Madygella* Rasnitsyn, 1969 based on the sclerotized pterostigma, SC and RS venations. However, the presence of a plesiomorphic character state in *Magnicapitixyela*, such as the 3r and 4r cells separate, which instead are merged in *Madygella*, indicates that *Magnicapitixyela* is a basal lineage to *Madygella*.

Neuropterida. Seven fossils assigned to the superorder Neuropterida have been recovered (Fig. 3B). One of them is specifically attributable to the Permian family †Permithonidae¹⁹ while the other six were assigned to the superorder based on the general habitus, the wing shape and venational pattern, even if the autapomorphies of the superorder are not visible⁵⁹. The latter fossils differ from each other in size (ranging from ~2.4 mm to ~6.4 mm) and in wing shape and venation. Based on these features these specimens can be considered as belonging to different taxa, indicating a high diversity of Neuropterida in the MSG fossil insect fauna. The †Permithonidae fossil represents the first complete specimen of this extinct Permian family¹⁹, which until now was known only from single forewings. Moreover, this finding expands the presence of the family well after the EPME events, which is in agreement with the previously formulated hypothesis where global-scale events, other than those occurring at the end of the Permian, could have promoted the insects faunal turnover from Paleozoic to Mesozoic. These fossils can be of interest in refining the phylogenetic placement of Neuropterida lineages, which has been debated for years^{60,61}, including the relevant families †Permithonidae and †Permosialidae that are still in the status of *incertae sedis*⁶² due to the insufficient fossil record.

Coleoptera. The Coleoptera assemblage of the MGS consists of well-known lineages of the Triassic fauna, with specimens belonging to Archostemata and Adephaga (Fig. 3C–E). Interestingly, a representative of the Polyphaga was also recovered in this assemblage as in Val Mara Site D (5).

Amphiesmenoptera. The fossils assigned to this taxon (Fig. S9) likely represent a stem group of Lepidoptera since they present apomorphies of

this order such as the forewings with 3-branched M vein, but also some other characters in conflict with this assignment (i.e., angle between M1 and M2 veins not greater than 60°)⁶³. These fossils can be of interest for clarifying the early evolutionary history of Amphiesmenoptera and in particular that of the Lepidoptera which remains unclear due to the scarcity of fossil records from the Mesozoic. Indeed, phylogenomic analyses estimated the last common ancestor of Trichoptera and Lepidoptera dates back to the Late Triassic¹⁰, while the first fossil definitively ascribable to Lepidoptera is of the Middle Jurassic⁶⁴.

Diptera. The dipteran assemblage here described can be considered unique, both in terms of taxa and individuals. Indeed, compared to the major Triassic dipteran fossiliferous sites of Grès à Voltzia, whose community includes principally immature stages and well-preserved isolated adult wings^{65,66}, the MSG assemblage consists mostly of complete, or almost complete well-preserved adults of different taxa and two exarate pupae (Figs. 4, 5, S11). Besides the richness of the MSG dipteran community, it is worth noting the non-random presence of round-shaped bodies on the last abdominal urites in 11 out of 54 adult individuals (Fig. 5). Due to their location and shape, these structures possibly represent seminal capsules, but since they seem to adhere externally to the insect bodies they could also be *Reticulatisporites*-like spores. If further structural analyses confirm the latter hypothesis, this finding would represent the oldest evidence of dipteran mediated transport of plant spores. Previous fossil evidence of Diptera actively transporting plant reproductive cells refers in fact to Early Cretaceous brachycerans, which were found with sparse pollen grains on their heads and mouthparts⁶⁷. This discovery, together with the elongated mouthparts of some of the collected fossils, allows hypothesizing that an insect-Lycopodiopsida interaction is a precursor association that was co-opted in the evolution of entomophily in gymnosperms and later angiosperms^{12,68–75}.

Conclusion

The MSG Val Mara VM12 insect fossil assemblage is significant for several reasons. Besides the exceptional preservation of the discovered fossils, which include insect groups considered rare in Triassic deposits such as Thysanoptera and Diptera, with fine morphological details like small cilia and ommatidia facets, the evolutionary implications of some of the discovered taxa is noteworthy. Among them are representatives of major lineages previously thought to have gone extinct with the EPME events, such as †Monura and †Permithonidae, and a blattodean bearing an external ootheca along with a well-developed sword-shaped ovipositor, which is crucial for understanding roachoid to cockroach transition and the evolution of maternal brood care. Additionally, some of the discovered fossils represent the first occurrence of their group, thereby backdating the origin of many insect taxa. For example, the discovered naiaid extends the fossil record of Anisoptera by approximately 40 My, and the hymenopteran *Magnicapitixyela dilettae* gen. sp. n. is the oldest sawfly and the first discovered in European deposits.

Together, these findings, coupled with the high diversity of insects assessed at Val Mara site VM12 (with a specimens-to-major lineages ratio of 13.1) and the evolutionary importance of the previous discoveries at MSG, highlight the global importance of the MSG deposit (Fig. 6B) for understanding the evolution of insects during the Triassic, a crucial period for insect fauna turnover.

Methods

Geological setting

The Middle Triassic carbonate succession of Monte San Giorgio (Switzerland-Italy; Fig. 1) belongs to the western termination of the Southern Alps and has been included in the UNESCO World Heritage List (WHL) because of its unique paleontological character of exceptionally well-preserved fossil fishes and marine reptiles e.g.^{26,76}. The site where the fossils were excavated is located in the valley of the Gaggiolo River, also known as “Val Mara”, west of Meride village (Fig. 1). The fossiliferous levels yielding the insect fauna belong to the upper Kalkschieferzone, late Ladinian in age¹⁷. The investigated section consists of an alternation of thin-bedded laminated limestones and marly limestones with subordinate marlstones and calcareous marlstones.

Fossil preparation

Three small excavations were started in the summer of 2020 and autumn in 2023 by the Museo cantonale di storia naturale (MCSN) at the Val Mara VM12 site (45° 53' 26" N, 8° 56' 49" E), near Meride (Monte San Giorgio, Switzerland). The collected fossil material was prepared using a steel needle under a stereomicroscope (Leica M80) and high-quality pictures acquired using an Olympus UC50 camera coupled with Olympus SZX 12 binocular microscope. Post-processing images were performed with Adobe Photoshop CS2.

Statistics and reproducibility

To exclude the random association of enigmatic round-shaped bodies with pleciofungivoridae-like individuals due to their presence in the fossil matrix, the following image-based analysis was performed. The number of round-shaped bodies attached to the abdomen of twelve individuals was compared with the mean number of round-shaped bodies in the fossil matrix. The mean number of round-shaped bodies in the fossil matrix was derived by counting the spores present over ten randomly selected unitary surfaces of 4 cm² of each fossil matrix (Table S1). Differences in round-shaped body abundance between the fossil matrix and the insect body were assessed with a Wilcoxon rank sum test⁷⁷. Shapiro's test was used to assess data normality previous to this analysis⁷⁸.

Terminology of the longitudinal veins, crossveins and cells adopted in the description of the new taxon follows Carpenter (1992)⁷⁹, adapted from Rasnitsyn (1969)⁸⁰. The terminology adopted in the text and figures for chronostratigraphy refers to the International Chronostratigraphic Chart v2023/09⁸¹.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data are available in the main text or the supplementary materials. Specimens are deposited at the Museo cantonale di storia naturale (Lugano, Switzerland) with the following specimen numbers: MCSN 8666-8681, 8683, 8686-8699, 8703-8706. High-quality images included in Supplementary are available in Montagna et al.⁸².

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References

- Benton, M. J. The origins of modern biodiversity on land. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 3667–3679 (2010).
- Raup, D. M. Size of the Permo-Triassic bottleneck and its evolutionary implications. *Science* **206**, 217–218 (1979).
- Song, H. J., Wignall, P. B., Tong, J. & Yin, H. Two pulses of extinction during the Permian-Triassic crisis. *Nat. Geosci.* **6**, 52–56 (2013).
- Nowak, H., Schneebeli-Hermann, E. & Kustatscher, E. No mass extinction for land plants at the Permian-Triassic transition. *Nat. Commun.* **10**, 384 (2019).
- Montagna, M. et al. Recalibration of the insect evolutionary time scale using Monte San Giorgio fossils suggests survival of key lineages through the End-Permian Extinction. *Proc. R. Soc. B* **286**, 20191854 (2019).
- Schachat, S. R. & Labandeira, C. C. Are insects heading toward their first mass extinction? Distinguishing turnover from crises in their fossil record. *Ann. Entomol. Soc. Am.* **114**, 99–118 (2021).
- Labandeira, C. C. & Sepkoski, J. J. Insect diversity in the fossil record. *Science* **261**, 310–315 (1993).
- Grimaldi, D. & Engel, M. S. *Evolution of the Insects* (Cambridge Univ. Press, 2005).
- Labandeira, C. C. Silurian to Triassic plant and insect clades and their associations: new data, a review, and interpretations. *Arthropod Syst. Phylogeny* **64**, 53–94 (2006).

10. Misof, B. et al. Phylogenomics resolves the timing and pattern of insect evolution. *Science* **346**, 763–767 (2014).
11. Zheng, D. et al. Middle-Late Triassic insect radiation revealed by diverse fossils and isotopic ages from China. *Sci. Adv.* **4**, eaat1380 (2018).
12. Labandeira, C. C. The pollination of mid Mesozoic seed plants and the early history of long-proboscid insects. *Ann. Missouri Bot. Gard.* **97**, 469–513 (2010).
13. Jouault, C., Nel, A., Perrichot, V., Legendre, F. & Condamine, F. L. Multiple drivers and lineage-specific insect extinctions during the Permo-Triassic. *Nat. Commun.* **13**, 7512 (2022).
14. Fowler, M. S. Extinction cascades and the distribution of species interactions. *Oikos* **119**, 864–873 (2010).
15. Jonsson, T., Karlsson, P. & Jonsson, A. Food web structure affects the extinction risk of species in ecological communities. *Ecol. Modell.* **199**, 93–106 (2006).
16. Renesto, S., Magnani, F. & Stockar, R. A new coelacanth specimen with elongate ribs from the Middle Triassic (Ladinian) Kalkschieferzone of Monte San Giorgio (Canton Ticino, Switzerland). *Riv. Ital. Paleontol. Stratigr.* **127**, 689–700 (2021).
17. Stockar, R., Baumgartner, P. O. & Condon, D. Integrated Ladinian biochronostratigraphy and geochronology of Monte San Giorgio (Southern Alps, Switzerland). *Swiss J. Geosci.* **60**, 239–269 (2012).
18. Béthoux, O. & Wieland, F. Evidence for Carboniferous origin of the order Mantodea (Insecta: Dictyoptera) gained from forewing morphology. *Zool. J. Linn. Soc.* **156**, 79–113 (2009).
19. Montagna, M., Magoga, G. & Magnani, F. The Middle Triassic palaeontomofauna of Monte San Giorgio with the description of *Merithone laetitiae* (†Permithonidae) gen. et sp. nov. *Swiss J. Paleontol.* **143**, 17 (2024).
20. Krzeminski, W. & Lombardo, C. New fossil Ephemeroptera and Coleoptera from the Ladinian (Middle Triassic) of Canton Ticino (Switzerland). *Riv. Ital. Paleontol. Stratigr.* **107**, 69–78 (2001).
21. Bechly, G. & Stockar, R. The first Mesozoic record of the extinct apterygote insect genus *Dasyleptus* (Insecta: Archaeognatha: Monura: Dasyleptidae) from the Triassic of Monte San Giorgio (Switzerland). *Palaeodiversity* **4**, 23–37 (2011).
22. Strada, L., Montagna, M. & Tintori, A. A new genus and species of the family Trachypachidae (Coleoptera, Adephaga) from the upper Ladinian (Middle Triassic) of Monte San Giorgio. *Riv. Ital. Paleontol. Stratigr.* **120**, 183–190 (2014).
23. Montagna, M. et al. Central nervous system and muscular bundles preserved in a 240 million year old giant bristletail (Archaeognatha, Machilidae). *Sci. Rep.* **7**, 46016 (2017).
24. Montagna, M., Strada, L., Dioli, P. & Tintori, A. The Middle Triassic lagerstätte of Monte San Giorgio reveals the oldest lace bugs (Hemiptera: Tingidae): *Archetingis ladinica* gen. n. sp. n. *Riv. Ital. Paleontol. Stratigr.* **124**, 35–44 (2018).
25. Tintori, A. The actinopterygian fish *Prohalecites* from the Triassic of N Italy. *Palaeontology* **33**, 155–174 (1990).
26. Montagna, M. Comment on *Phylogenetic analyses with four new Cretaceous bristletails reveal inter-relationships of Archaeognatha and Gondwana origin of Meinertellidae*. *Cladistics* **36**, 227–231 (2020).
27. Rinehart, L. F., Rasnitsyn, A. P., Lucas, S. G. & Heckert, A. B. Instar sizes and growth in the Middle Permian monuran *Dasyleptus brongniarti* (Insecta: Machilida: Dasyleptidae). *Bull. N M Mus. Nat. Hist. Sci.* **30**, 270–272 (2005).
28. Bashkuev, A. et al. Insects from the Buntsandstein of Lower Franconia and Thuringia. *PalZ* **86**, 175–185 (2012).
29. Simms, M. J. & Ruffell, A. H. Synchronicity of climatic change and extinctions in the Late Triassic. *Geology* **17**, 265–268 (1989).
30. Dal Corso, J. et al. Extinction and dawn of the modern world in the Carnian (Late Triassic). *Sci. Adv.* **6**, eaba0099 (2020).
31. Rozefelds, A. C. A fossil zygoteran nymph (Insecta: Odonata) from the Late Triassic Aberdare conglomerate: Southeast Queensland. *Proc. R. Soc. Qld.* **96**, 25–32 (1985).
32. Nel, A., Nam, G. S. & Jouault, C. First representative of the odonatan superfamily Triassolestoidea (Odonoptera: Parazygoptera) from the Upper Triassic of the Korean Peninsula. *Alcheringa* **46**, 237–243 (2022).
33. Kukalová-Peck, J. Carboniferous protodonatoid dragonfly nymphs and the synapomorphies of Odonoptera and Ephemeroptera (Insecta: Palaeoptera). *Palaeodiversity* **2**, 169–198 (2009).
34. Fleck, G. et al. Phylogeny and classification of the Stenophlebiptera (Odonata: Epiproctophora). *Ann. Soc. Entomol. Fr.* **39**, 55–59 (2003).
35. Kohli, M. et al. Evolutionary history and divergence times of Odonata (dragonflies and damselflies) revealed through transcriptomics. *iScience* **24**, 103324 (2021).
36. McKittrick, F. A. Evolutionary study of cockroaches. *Cornell Univ. Agric. Exp. Sta. Mem.* **389**, 1–197 (1964).
37. Klass, K. D. The ovipositor of Dictyoptera (Insecta): homology and ground-plan of the main elements. *Zool. Anz.* **236**, 69–101 (1998).
38. Anisutkin, L. D. et al. Fossil insects in the Cretaceous mangrove facies of southern Negev, Israel in *Plant-arthropod interactions in the early Angiosperm history: evidence from the Cretaceous of Israel* (eds. Krassilov, V. & Rasnitsyn, A.) 190–223 (Pensoft, 2008).
39. Gao, T. et al. Maternal care by Early Cretaceous cockroaches. *J. Syst. Paleontol.* **17**, 379–391 (2019).
40. Hörnig, M. H., Haug, J. T. & Haug, C. New details of *Santanmantis axelrodi* and the evolution of the mantodean morphotype. *Palaeodiversity* **6**, 157–168 (2013).
41. Pinto, I. D. & Purper, I. A N. *blattoid Cretac. Braz. Pesqui. geociênc* **18**, 5–10 (1986).
42. Bechly, G. “Blattaria”: cockroaches and roachoids in *The Crato fossil beds of Brazil: window into an ancient world* (eds. Martill, D. M., Bechly, G. & Loveridge, R. F.) 239–249 (Cambridge Univ. Press, 2007).
43. Hörnig, M. K., Haug, C., Schneider, J. W. & Haug, J. T. Evolution of reproductive strategies in dictyopteran insects—clues from ovipositor morphology of extinct roachoids. *Acta Paleontol. Pol.* **63**, 1–24 (2018).
44. Vršansky, P., Vishniakova, V. N. & Rasnitsyn, A. P. Blattida in *History of insects* (eds. Rasnitsyn, A. P. & Quicke, D. L. J.) 263–270 (Kluwer, 2002).
45. Du, E. et al. Convergent adaptation of ootheca formation as a reproductive strategy in polyneoptera. *Mol. Biol. Evol.* **39**, msac042 (2022).
46. Fraser, N. C., Grimaldi, D. A., Olsen, P. E. & Axsmith, B. A Triassic Lagerstätte from eastern North America. *Nature* **380**, 615–619 (1996).
47. Grimaldi, D. A., Shmakov, A. & Fraser, N. Mesozoic thrips and early evolution of the order Thysanoptera (Insecta). *Int. J. Paleopathol.* **78**, 941–952 (2004).
48. Shcherbakov, D. E. The earliest true bugs and aphids from the Middle Triassic of France (Hemiptera). *Russ. Entomol. J.* **19**, 179–182 (2010).
49. Criscione, J. & Grimaldi, D. A. The oldest predaceous water bugs (Insecta, Heteroptera, Belostomatidae), with implications for paleolimnology of the Triassic Cow Branch Formation. *J. Paleontol.* **91**, 1166–1177 (2017).
50. Johnson, K. P. et al. Phylogenomics and the evolution of hemipteroid insects. *Proc. Natl. Acad. Sci. USA* **115**, 12775–12780 (2018).
51. Rasnitsyn, A. P. New Triassic Hymenoptera from Central Asia. *Paleontologicheskij Zh.* **1**, 88–96 (1964).
52. Rasnitsyn, A. P. New Xylidae (Hymenoptera) from the Mesozoic of Asia. *Paleontologicheskij Zh.* **4**, 69–85 (1966).
53. Kopylov, D. S. New sawflies of the subfamily Madygellinae (Hymenoptera, Xyelidae) from the Middle-Upper Triassic of Kyrgyzstan. *Paleontol. J.* **48**, 610–620 (2014).
54. Riek, E. F. Fossil insects from the Triassic beds at Mt. Crosby, Queensland. *Aust. J. Zool.* **3**, 654–691 (1955).
55. Engel, M. S. A new sawfly from the Triassic of Queensland (Hymenoptera: Xyelidae). *Mem. Queensl. Mus.* **51**, 558 (2005).
56. Schlüter, T. *Moltenia riekii* n. gen., n. sp. (Hymenoptera: Xyelidae?), a tentative sawfly from the Molteno Formation (Upper Triassic), South Africa. *PalZ* **74**, 75–78 (2000).

57. Lara, M. B., Rasnitsyn, A. P. & Zavattieri, A. M. *Potrerilloxyela menendezi* gen. et sp. nov. from the Late Triassic of Argentina: the oldest representative of Xyelidae (Hymenoptera: Symphyta) for Americas. *Paleontol. J.* **48**, 182–190 (2014).
58. Oyama, N. & Maedo, H. *Madygella humioi* sp. nov. from the Upper Triassic Mine Group, southwest Japan: The oldest record of a sawfly (Hymenoptera: Symphyta) in East Asia. *Paleontol. Res.* **24**, 64–71 (2020).
59. Bechly, G. 11.16 Neuropterida: snakeflies, dobsonflies and lacewings in *The Crato fossil beds of Brazil: window into an ancient world* (eds. Martill, D. M., Bechly, G. & Loveridge, R. F.) 328–340 (Cambridge Univ. Press, 2007).
60. Shcherbakov, D. E. Permian ancestors of Hymenoptera and Raphidioptera. *ZooKeys* **358**, 45–67 (2013).
61. Vasilikopoulos, A. et al. An integrative phylogenomic approach to elucidate the evolutionary history and divergence times of Neuropterida (Insecta: Holometabola). *BMC Evol. Biol.* **20**, 64 (2020).
62. Martins, C. C. et al. A world checklist of extant and extinct species of Megaloptera (Insecta: Neuropterida). *Eur. J. Taxon.* **812**, 1–93 (2022).
63. Zhang, W. et al. New fossil Lepidoptera (Insecta: Amphiesmenoptera) from the Middle Jurassic Jiulongshan Formation of Northeastern China. *PLoS ONE* **8**, e79500 (2013).
64. Sohn, J. C., Labandeira, C. C. & Davis, D. R. The fossil record and taphonomy of butterflies and moths (Insecta, Lepidoptera): implications for evolutionary diversity and divergence-time estimates. *BMC Evol. Biol.* **15**, 12 (2015).
65. Krzeminski, W., Krzeminska, E. & Papier, F. *Grauvogelia arzwilleriana* sp. n. - the oldest Diptera species (Lower/Middle Triassic of France). *Acta Zool. Cracov.* **37**, 95–99 (1994).
66. Marchal-Papier, F. Les insectes du Buntsandstein des Vosges (NE de la France). Biodiversité et contributions aux modalités de la crise biologique du Permo-Trias, *Ph. D. thesis* (Université Louis Pasteur, 1998).
67. Labandeira, C. C., Kvaček, J. & Mostovski, M. B. Pollination drops, pollen, and insect pollination of mesozoic gymnosperms. *Taxon* **56**, 663–695 (2007).
68. Peñalver, E. et al. Long-proboscid flies as pollinators of Cretaceous gymnosperms. *Curr. Biol.* **14**, 1917–1923 (2015).
69. Labandeira, C. C. et al. The evolutionary convergence of mid-Mesozoic lacewings and Cenozoic butterflies. *Proc. R. Soc. B* **283**, 20152893 (2016).
70. Peris, D. et al. False blister beetles and the expansion of gymnosperm-insect pollination modes before angiosperm dominance. *Curr. Biol.* **27**, 897–904 (2017).
71. Cai, C. et al. Beetle pollination of cycads in the Mesozoic. *Curr. Biol.* **28**, 2806–2812 (2018).
72. Liu, Q. et al. High niche diversity in Mesozoic pollinating lacewings. *Nat. Commun.* **9**, 1–11 (2018).
73. Lin, X. et al. Life habits and evolutionary biology of new two-winged long-proboscid scorpionflies from mid-Cretaceous Myanmar amber. *Nat. Commun.* **10**, 1235 (2019).
74. Peris, D. et al. Generalist pollen-feeding beetles during the mid-Cretaceous. *iScience* **23**, 100913 (2020).
75. Zhao, X. et al. Mouthpart homologies and life habits of Mesozoic long-proboscid scorpionflies. *Sci. Adv.* **6**, 1259 (2020).
76. Lombardo, C., Tintori, A. & Tona, D. A new species of *Sangiorgioichthys* (Actinopterygii, Semionotiformes) from the Kalkschieferzone of Monte San Giorgio (Middle Triassic; Meride, Canton Ticino, Switzerland). *Boll. Soc. Paleontol. Ital.* **51**, 203–212 (2012).
77. Wilcoxon, F. Individual comparisons by ranking methods. *Biometrics* **1**, 80–83 (1945).
78. Shapiro, S. S. & Wilk, M. B. An analysis of variance test for normality (complete samples). *Biometrika* **52**, 591–611 (1965).
79. Carpenter, F. M. *Treatise on Invertebrate Paleontology. Part R. Arthropoda 4, Volume 4: Superclass Hexapoda* (The University of Kansas and The Geological Society of America, 1992).
80. Rasnitsyn, A. P. Proiskhozhdenie i ehvolyutsiya nizshikh pereponchatokrylykh [The origin and evolution of lower Hymenoptera]. *Tr. Paleontologicheskogo Inst. Akademii Nauk SSSR* **123**, 1–196 (1969).
81. Cohen, K. M., Finney, S. C., Gibbard, P. L. & Fan, J. X. The ICS International Chronostratigraphic Chart. *Episodes* **36**, 199–204 (2013).
82. Montagna, M., Magoga, G., Stockar, R. & Magnani, F. The contribution of the Middle Triassic fossil assemblage of Monte San Giorgio to insect evolution. <https://figshare.com/s/c189f7a192b9b29bc03c>.

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Author contributions

Conceptualization: M.M.; Fieldwork activity: F.M., R.S.; Fossils preparation and image acquisition: F.M.; Fossil analyses: M.M., G.M., F.M.; Images and statistical analyses: M.M., G.M.; Writing—original draft: M.M., G.M.; Writing—review & editing: M.M., G.M., F.M., R.S.

Competing interests

The authors declare no competing interests.

Additional information

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