

NEW FOSSIL EPHEMEROPTERA AND COLEOPTERA FROM THE LADINIAN (MIDDLE TRIASSIC) OF CANTON TICINO (SWITZERLAND)

WIESLAW KRZEMINSKI* & CRISTINA LOMBARDO**

Received August 29, 2000; accepted January 8, 2001

Key-words: Ephemeroptera, Coleoptera, new taxon, Middle Triassic, Switzerland.

Riassunto. Vengono qui descritti due insetti provenienti dai sedimenti del Ladinico superiore (Triassico Medio) di Meride (Canton Ticino, Svizzera). *Tintorina triassica* gen. n. sp. n., un rappresentante di una nuova famiglia, Tintoriniidae, degli Ephemeroptera, viene descritto sulla base di due esemplari, uno dei quali quasi completo; una singola elitra viene invece attribuita a *Notocupes* sp. ind. (Cupedidae, Coleoptera). Al di là dell'interesse tassonomico del ritrovamento, si deve sottolineare come questi siano i primi insetti ritrovati nell'area del Monte San Giorgio-Besano, famosa soprattutto per i vertebrati. La presenza degli Ephemeroptera conferma la presenza di acqua dolce sulla terraferma in prossimità dei bacini dove era possibile la conservazione di molti organismi.

Abstract. Two insects are described from the sediments of the uppermost Ladinian (Middle Triassic) of Meride (Canton Ticino, Switzerland). *Tintorina triassica* gen. n. sp. n., a representative of a new family, Tintoriniidae, of the Ephemeroptera, is described on the basis of two specimens, one being almost complete; a single elytron is ascribed to *Notocupes* sp. ind. (Cupedidae, Coleoptera). The ephemeroptera specimens possibly belong to a previously unrecognized Triassic suborder/order within the infraorder Ephemeroidea. Apart from the taxonomic interest of this find, it is pointed out that these are the first fossil insects found in the classic deposits of Monte San Giorgio-Besano, famous mostly for its vertebrates. The presence of Ephemeroptera confirms the existence of land with adjacent freshwater basins where the preservation of many organisms in fine-grained matrix was possible.

Introduction.

In Triassic sediments of Western Europe insects, most of which are not yet described, are rare. The most abundant insect collection from these basins, consisting of ca. 5300 specimens (Marchal-Papier 1998), was inventoried by Louis Grauvogel and Jean-Claude Gall from the Vosges Mountains (Alsace, France). The first insect from this locality was described by Handlirsch (1918); succeeding descriptions were made by Grauvogel & Laurentiaux (1952), Laurentiaux (1953), Krzeminski et

al. (1994), Krzeminski & Krzeminska (1996), Papier & Grauvogel-Stamm (1995) and Papier et al. (1996, 1997).

Other known Western European Triassic fossil localities, among others, occur in Portugal (Texeira 1947), Spain (Via & Calzada 1987), Switzerland (Geyer & Kelber 1987), France (Fliche 1901; Meunier 1907; Ellenberg et al. 1952; Nel 1989), Italy (Whalley 1986; Bechly 1997), Germany (Kühn 1838; Heer 1864; Sandberger 1867; Roemer 1876; Zeuner 1930; Brauckman & Schlüter 1993) and Great Britain (Krzeminski & Jarzembowski 1999). Fossil insect occurrences from Eastern Europe, principally from the latest Permian through the Triassic, are reviewed by Ponomarenko & Sukacheva (1998), and for fossil Coleoptera, by Ponomarenko (1969).

Recently, at the Middle Triassic locality of Meride, in Switzerland, the remnants of three insects were found. The first two specimens represent a new family for the order Ephemeroptera and the third belongs to the coleopteran genus *Notocupes* Ponomarenko, (Cupedidae).

Until now, only one species of Triassic larval mayfly has been described from Europe (Handlirsch 1918).

Triassic beetle fossils have been recorded by Fliche (1901), Whalley (1986), Via & Calzada (1987), Brauckman & Schlüter (1993) and Ponomarenko (1969).

Historical and geological remarks.

The famous paleontological area of Monte S. Giorgio-Besano, located at the Italy-Switzerland boundary between Varese and Lugano (Fig. 1), has yielded since the last century some of the most interesting Middle Triassic levels with vertebrate fossils (Kuhn-Schneider 1974; Tintori et al. 1985; Bürgin et al. 1989; Sander 1989). The deposits yielding these fossil vertebrates

* Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, ul. Sławkowska 17, 31-016 Kraków, Poland.

**Dipartimento di Scienze della Terra, Università degli Studi, Via Mangiagalli 34, 20133 Milano, Italy.

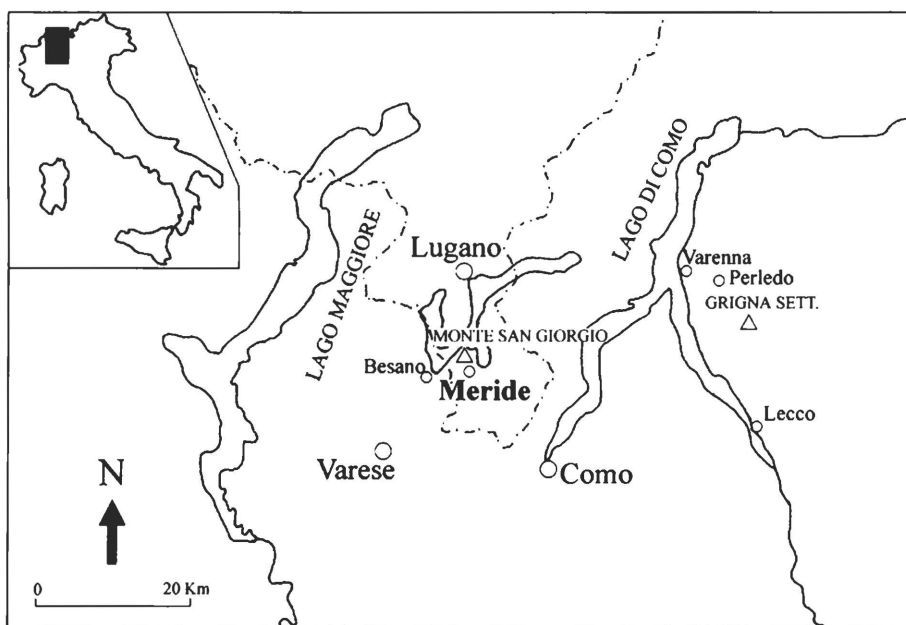


Fig. 1 - Map of the Monte San Giorgio area.

include the Besano Formation (Grenzbitumenzone of Swiss Authors) and the overlying Meride Limestone in both its lower and uppermost part (the Kalkschieferzone). These levels date back from the Anisian-Ladinian boundary to the latest Ladinian (Fig. 2).

The Monte San Giorgio area is unique stratigraphically for the possibility of following the evolution of fishes, reptiles and crustaceans during a time span of about 7-8 million years, as thousands of specimens have been collected since the last century. This is the result of industrial exploitation of bituminous shales as a source of energy and for the production of drugs (Stoppani 1857; Bassani 1886; Repossi 1909), and of paleontological excavations in several sites. In the last few years, new fossiliferous horizons have been excavated in order to stratigraphically separate the faunas (Furrer 1995; Bürgin 1995; Tintori & Lombardo 1999); field work is still in progress for the Besano Formation by the Museo Civico di Storia Naturale di Milano on the Italian side and for the lower Meride Limestone by Swiss team from the Paläontologisches Institut und Museum der Universität in Zürich (PIMUZ) and the Museo Cantonale di Storia Naturale di Lugano (MCSN) (Furrer 1995; Teruzzi & Dal Sasso 1995; Bürgin 1998).

With regard to the upper Meride Limestone, particular attention has been paid in the last few years by the Dipartimento di Scienze della Terra of Milano University (DSTUM) to the youngest levels (the so called Kalkschieferzone), which have been assigned to uppermost Ladinian, based on palynological assemblages (Scheuring 1978). Geochemical and paleobotanical studies are in progress to improve the definition of the unit. Wirz (1945) mentioned for the first time the presence of plant, crustacean and fish remains in different levels of this unit, which crop out along the Val Mara (Gaggiolo

creek) near Meride. However, apart from the find of a small *Lariosaurus* and small actinopterygian fishes (Kuhn-Schnyder 1987; Bürgin 1992), no regular excavations had been carried out by Swiss paleontologists until 1994, when three small-scale excavations were carried out by the PIMUZ in the Val Mara (Furrer 1995; Bürgin 1995). On the Italian side, a few fishes were collected at the beginning of the this century (De Alessandri 1910) near Ca' del Frate (now Besnasca, Viggiù, VA), but it has been only since the beginning of the 1980's that systematic field work has been conducted by the DSTUM in conjunction with the Civico Museo Insubrico di Storia Naturale di Induno Olona at that site. Several hundred fishes, together with a few specimens of the nothosaur *Lariosaurus* and thousands of two kinds of crustaceans have been collected during several field seasons (Tintori & Renesto 1983, 1990; Tintori 1990a, b; Renesto 1993; Lombardo 1997, 1999).

In 1997, field work at the upper part of the lower Kalkschieferzone of Val Mara was started by the MCSNL and the DSTUM. This fossiliferous horizon is somewhat older than that of Ca' del Frate and it is placed between layer 102 of Scheuring (1978) and layer 60 of Wirz (1945), representing a thickness of 450 cm. The sequence consists of massive (10-15 cm thick), apparently barren layers, which alternate with well-laminated, usually fossiliferous levels; thin layers of volcanic clay and abundant celestine also are present. Studies, that are still in progress, are examining the fish faunas from these different sites, which point to a peculiar distribution of varied faunal assemblages, particularly as the fish species have a non-homogeneous stratigraphical distribution (Tintori et al. 1998; Lombardo et al. 1999; Lombardo 1999). Based on the data collected so far, these assemblages could be related both to age and vertical to

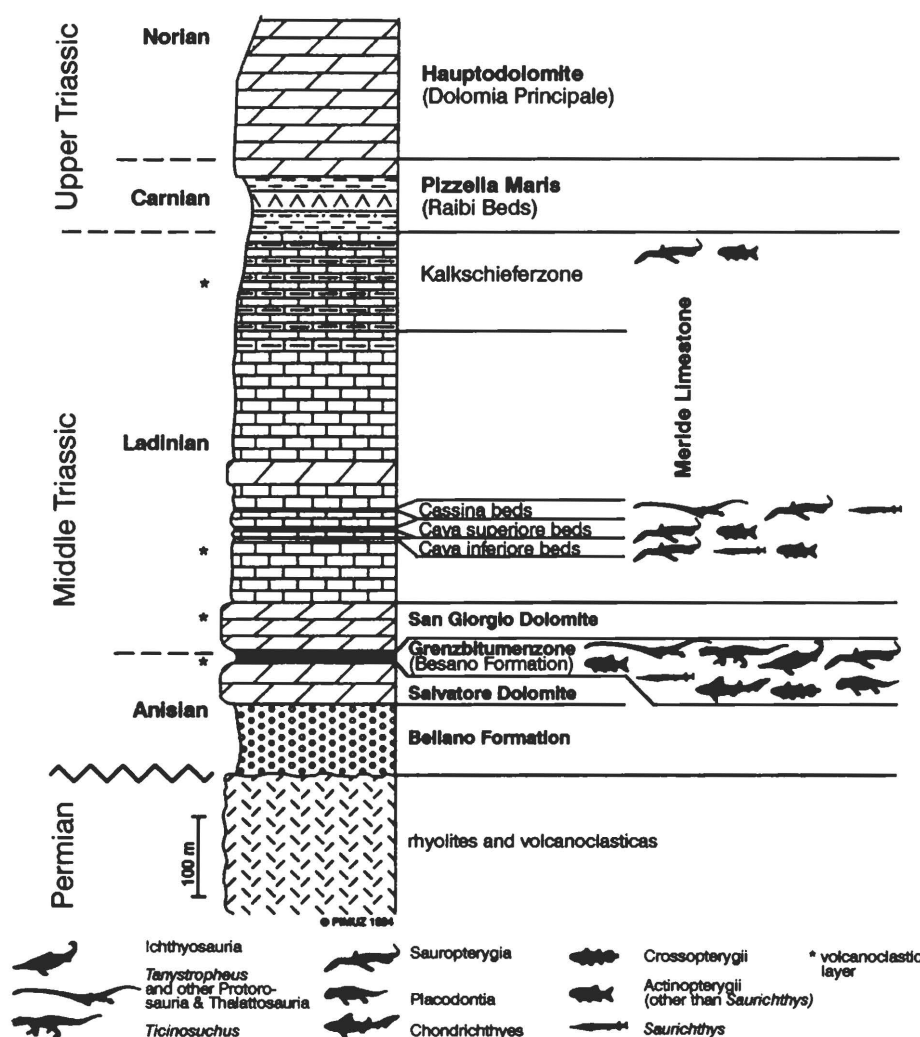


Fig. 2 - Stratigraphy of the Triassic sediments in the area of Monte San Giorgio (after Furrer, 1995).

lateral environmental changes (Tintori & Lombardo 1999; Lombardo 1999). The depositional environment for the Kalkschieferzone is interpreted as a shallow complex lagoon influenced by nearby emerged land, with wide fluctuation in temperature and water salinity. Important periodic flow of fresh water from adjoining land possibly lowered the water salinity of the basin (Tintori 1990a, b; Tintori & Renesto 1990), depositing numerous plant remains, especially conifers and conchostracan crustaceans, which currently are freshwater dwellers (Tintori 1990a).

The discovery of the insect fossils, described herein, during field work in 1998 in the Kalkschieferzone of Val Mara, is remarkable as they are the first fossil insects to be found in Monte San Giorgio area in over 150 years of work in the area (Lombardo et al. 1998). Additionally, two more insect fossils were collected in 1999 by the PIMUZ team at Acqua del Ghiffo in the Lower Meride Limestone and further three specimens were found during July 2000 excavations in Val Mara. Thus, the whole Meride Limestone is becoming an important source of Middle Triassic insects, which are otherwise rather rare worldwide.

Materials and methods.

The material used in this study comes from the Kalkschieferzone (Upper Meride Limestone) of Val Mara (Canton Ticino, Switzerland); the specimens are preserved in quite well laminated marly limestones. Drawings were made using a binocular microscope with a draw tube attachment. The holotype (MCSN 4666) of *Tintorina meridensis* shows body partially preserved, the head being lost, while the thorax is completely preserved, with legs as fragments; two wings and five basal segments of abdomen are present. The second specimen (MCSN 5001) ascribed to this species, consists only of a wings pair and a fragment of the body. The beetle *Notocupes* sp. (MCSN 5002) is represented by a single elytron.

Paleontological descriptions.

Order Ephemeroptera Hyatt & Arms, 1890

All Ephemeroptera are biologically associated with a water environment, in which the larvae are oblig-

ately aquatic. Extant adults live close to water habitats, usually do not feed, and live only for a short period of time.

As the first mayflies are from the Upper Carboniferous, they are among the oldest insect orders. The radiation of Ephemeroptera began in the Upper Carboniferous (Kukalová-Peck 1985) and during that period they formed an abundant and ecologically important group, probably of worldwide distribution. Permian Ephemeroptera have been recorded by Tillyard (1932), Tchernova (1965), Kukalová (1968), Kinzelbach (1970), Riek (1976) and Carpenter (1992).

Ephemeropteran records from the Triassic are scarce. Riek (1976) erected a new family, Litophlebiidae (=Xenophlebiidae Riek), from the Upper Triassic of South Africa. Wing fragments of adult mayflies were found in Great Britain (Thompson 1965) and Spain (Via & Calzada 1987). These fossils are so badly preserved that a more precise identification is not possible. Ephemeropteran larvae have been found more frequently: Handlirsch (1918) described a larva from the Vosges Mountains (France; Anisian), and Via & Calzada (1987) from Spain.

Information on the Triassic Ephemeroptera can be found in the dissertations of Calafat (1988) from Spain and in Marchal-Papier (1998) from France, where there are camera lucida drawings of an adult mayfly and of some larvae, but without formal descriptions.

Both the drawing of Riek (1976) and one of the specimen figured by Marchal-Papier (1998) are very similar to the specimen described herein and differ only in essential details of wing venation, especially the length of subcosta and cubital veins.

Family Tintorinidae n. fam.

Figs. 3, 4, 5

Diagnosis. As for the species

Type genus: *Tintorina* n. gen., from the Middle Triassic of Switzerland, by monotypy.

Genus *Tintorina* n. gen.

Diagnosis: as for species

Type species: *Tintorina meridensis* n. sp., by monotypy.

Etymology: Dedicated to prof. Andrea Tintori, who is leading the paleontological research in the area.

Type locality: Meride, Switzerland; Middle Triassic.

Tintorina meridensis, n. sp.

Material. Holotype (MCSN 4666) and paratype (MCSN 5001) from Meride (Switzerland, Canton Ticino), Middle Triassic. Housed in the Museo Cantonale di Storia Naturale, Lugano (Switzerland).

Etymology: after the locality, Meride.

Diagnosis. Wings (Figs. 3; 4A, B; 5) with a characteristic, narrow base; both wings are narrow and long, with the forewing being only slightly longer. Sc very short, reaching shortly beyond the midlength. CuA divides into CuA1 and CuA2, while CuP is single; thus three cubital veins are present. Only one anal vein A1 present, in the forewing partially fused with Cu and CuP. In the hind wing A1 is free and terminates in wing margin. Legs thin and long (Fig. 4C).

Description. The description is based on the holotype (MCSN 4666); the other specimen, found during the July 2000 excavation at Val Mara (MCSN 5001), is poorly preserved but the venation pattern, quite well visible, allows to ascribe this specimen to this species.

Body partially preserved: head missing; thorax completely preserved, with legs as fragments; two wings (probably one fore- and one hindwing); five basal segments of abdomen. Terminal part of abdomen and genitalia not preserved (Fig. 3).

Wings (Figs. 3; 4A, B; 5): their position in relation to the body and the differences in their size, length/width proportions and venation indicate that one left forewing (11 x 3 mm) and one right hindwing (10 x 2,6 mm) are in reverse position. The venation is generally well preserved; only radial and medial fields are incomplete (for explanation of abbreviations see Fig. 4).

Costal margin of a forewing is straight, and of hindwing is slightly convex. Costa thick, strongly sclerotized, almost encircling the entire wing, with thick, strong bristles attached along the vein, except for a short anal section. Sc short, not reaching 2/3 of wing length and terminating opposite end of MA2. In Ephemeroptera Sc is only exceptionally reduced in length, and a short Sc is found for a first time in this group. A humeral vein (h), characteristic of Ephemeroptera (Fig. 6A), is absent in both wings. There are a few crossveins in the costal cell, viewed best on the distal part of the cell in fore wing. R1 well preserved over its entire length; cell Sc with crossveins only in its distal part. The veins of sector Rs are variously preserved in both wings; in the forewing almost all long veins are visible, while the crossveins are mostly obscure; in the hindwing only three long veins are fully preserved; of the 4th and 5th veins, only the basal sections are present, but the crossveins are well evident. Vein Rs relatively long; cell r1 is broad, especially at its medial part; basal section of this cell is almost devoid of crossveins (up to 1/3 its length); in the hind wing however, one crossvein is present in this region. In 1/3 of this cell a characteristic, sub-sinuuous, oblique crossvein is present; distal of this vein numerous, conspicuous crossveins occur in both wings.

The medial sector is well preserved in the forewing, with triads of medial veins and numerous crossveins within the cells. The hindwing possesses only a part of MA3 and the triad: MP1, IMP, MP2 is retained.

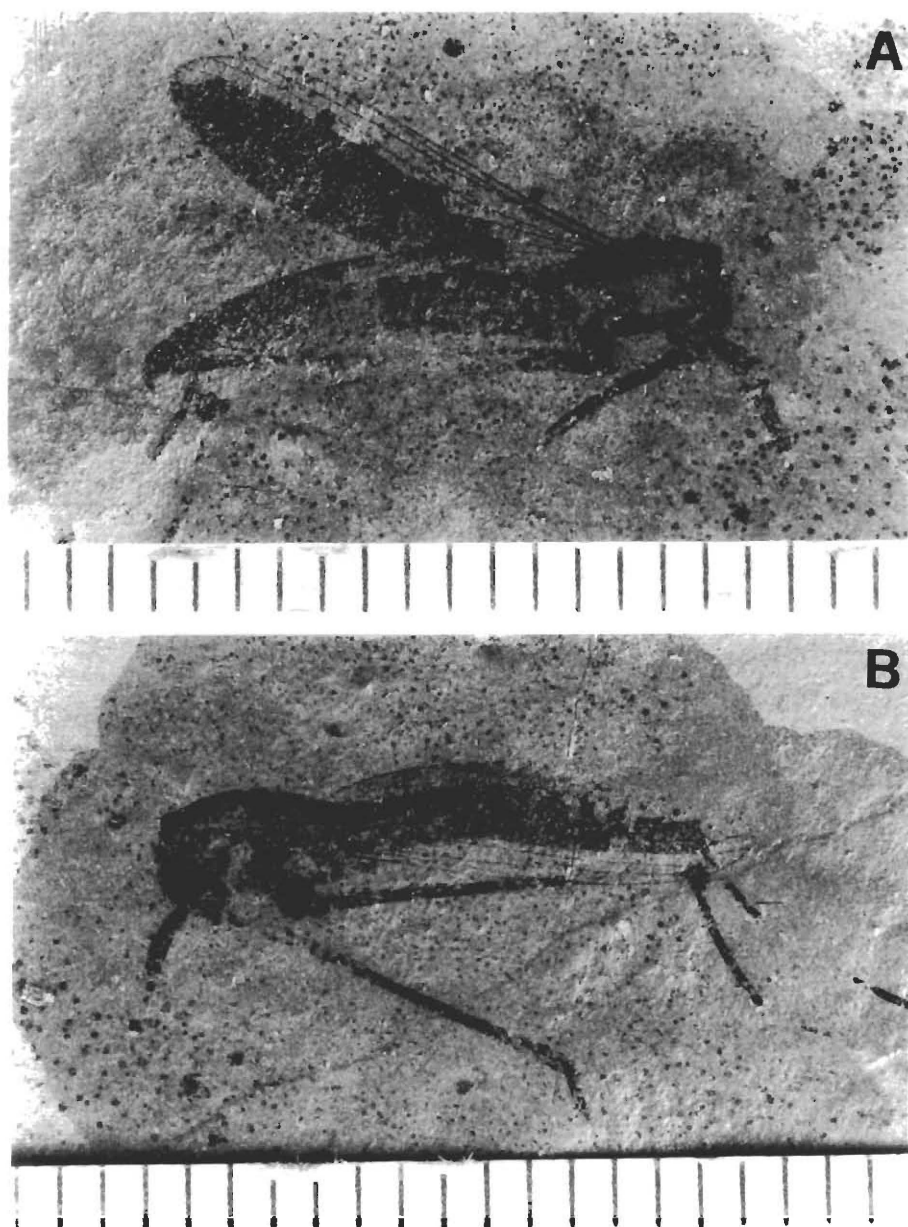


Fig. 3 - *Tintorina meridensis* n. sp. (MCSN 4666): A) the specimen on the slab; B) the counterslab.

Cubito-anal sectors in both wings are well preserved, and the differences between them are noticeable. In the forewing CuA2 is very short, because it is fused with CuA1 to form a long stem, more than three times as long as CuA2; in the hindwing CuA2 is long, more than twice as long as the stem with CuA1. CuP subsinuous and of almost equal length in both wings; originating from the common stem of Cu, formed by CuA1, CuA2 and CuP. Basal section of A1 in the forewing is fused with Cu, while the distal section is fused with CuP; medial part is delicate and looped. In the hindwing A1 is free, terminating at the wing margin. Crossveins of cubito-anal sector are present only in the cell MP2 of the forewing; in the hindwing they occur in the cells MP2, CuA1 and CuA2. The posterior and ventral area of both wings appears darker than the rest: this could be the trace of coloring, as wing color can be retained on these fossils, although not necessarily the original pattern.

However, the quite definite arrangement of this dark spot supports this interpretation, as well as its almost identical arrangement on the wings of the other specimen (MCSN 5001; Fig. 5).

Legs (Fig. 4C): Forelegs are relatively short through a strong reduction of a femur; mid- and hindlegs long and slender; femora and tibiae of all legs covered with short, strong bristles. The hindlegs are longest; one of which is completely preserved, twice as long as forewing. The trochanter is broad, oval; femur thick and long, tibia slender, long; tarsus probably 5-segmented, the last segment provided with small claws. The length of tarsal segments is difficult to estimate due to poor state of preservation. Most probably the first segment is short and each of three succeeding ones is ca. twice as long as its predecessor; the last tarsal segment is very short.

Abdomen. Only five basal segments are preserved.

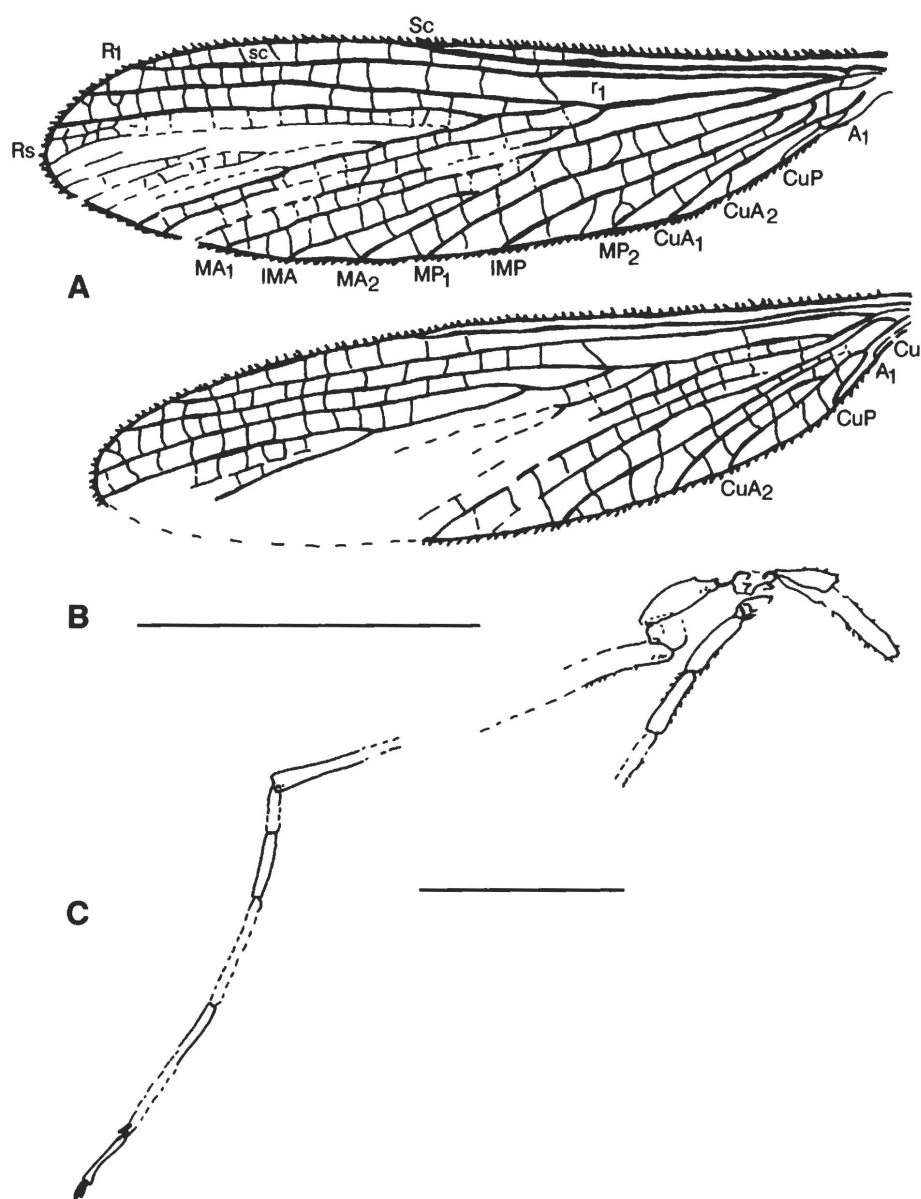


Fig. 4 - *Tintorina meridensis* n. sp. (MCSN 4666): A) forewing; B) hindwing C) legs. Scale bar: 5 mm. Abbreviations are: Sc: Subcosta, R: radius, Rs: Radial sector, MA: Anterior media, MP: Posterior media, CuA: Anterior cubitus, CuP: Posterior cubitus, A: Anal vein, h: Humeral vein, Cu: Cubitus, IMA: Intercalary Anterior Media.

the first being the shortest one and the following ones successively longer. No portions of the following segments are preserved, including the genitalia and the head; these body parts probably were dismembered while the insect was in water, prior to fossilization.

Discussion.

The specimen here described is one of the most interesting European Triassic insects. The general body shape and wing venation indicate its placement in the order Ephemeroptera. There are however characters of wing venation, which are unique to this and two other Triassic insects, which have been assigned to the Ephemeroptera. One of them is *Litophlebia oplata* Riek 1976 from South Africa (Fig. 6B). Originally described as *Xenophlebia oplata*, the name however was preoccupied and it was changed by Hubbard & Riek (1977) to

Litophlebia oplata (Litophlebiidae). The second specimen, currently undescribed, is from Vosges Mountains (Alsace, France), and it was figured by Marchal-Papier (1998) in her dissertation. All three wings, including those of *Tintorina meridensis* n. sp., are characterized by absence of the humeral vein, which is characteristic for the Ephemeroptera (Fig. 6B) and by the shorter Sc which is reduced to various degrees in these insects. The longest Sc is in *Litophlebia oplata*, and its length is still within the range of variation of the order. The specimen from Vosges Mountains has a markedly shorter Sc, but longer than in *Tintorina meridensis* n. sp., in which Sc is greatly reduced. These three insects may indicate the presence of a separate group of ephemeroid insects during the Triassic. However, the material is too scarce and poorly preserved. Our holotype (MCSN 4666) is the most complete of the three, having parts of body and legs and both wings preserved; the two other specimens are known only from single wings.

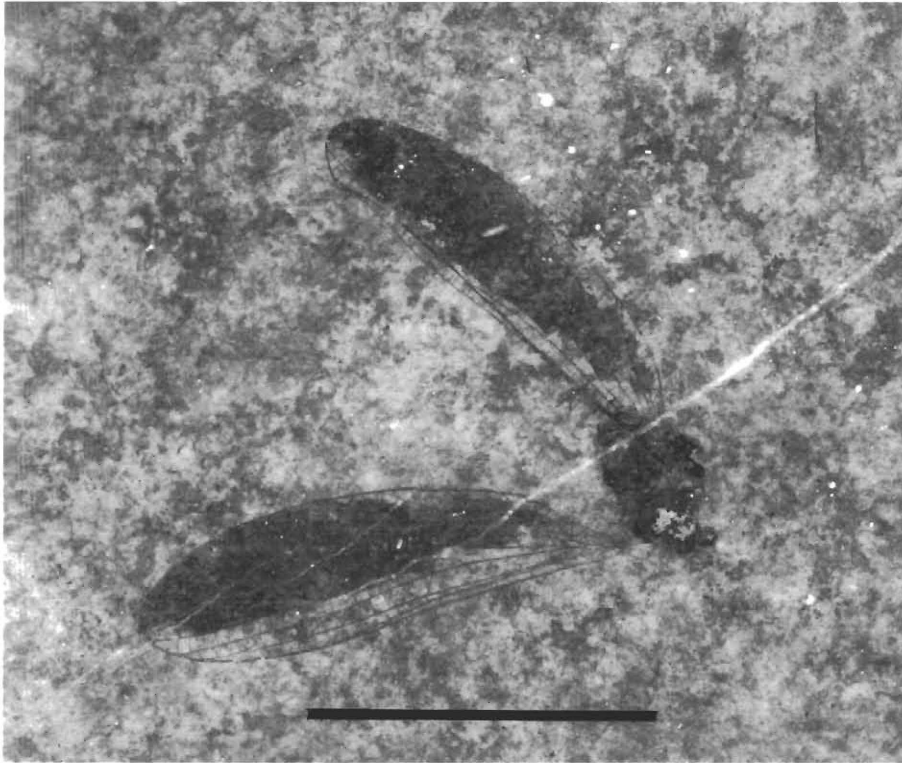


Fig. 5 - Wings of *Tintornia meridensis* n. sp. (MCSN 5001). Scale bar: 1 cm.

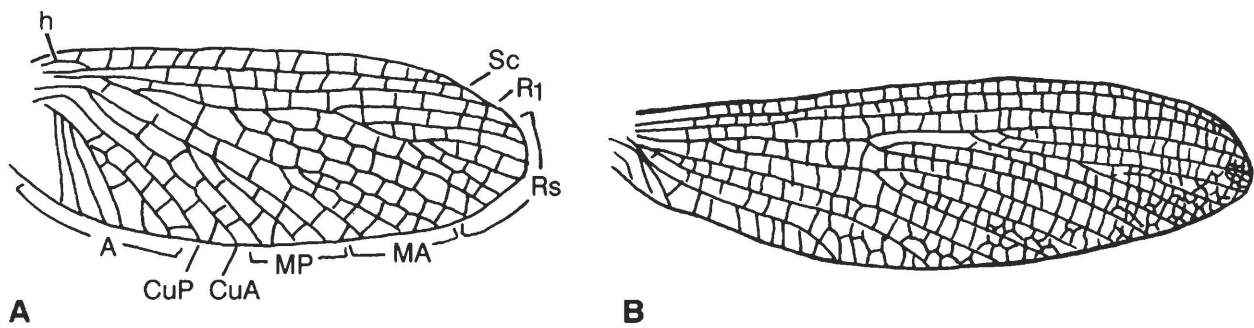


Fig. 6 - Wings of fossil Ephemeroptera: A) *Misthodotes edmundsi* Carpenter, Lower Permian (after Kinzelbach & Lutz 1984); B) *Litophebia oplata* Riek, Upper Triassic (after Riek 1976).

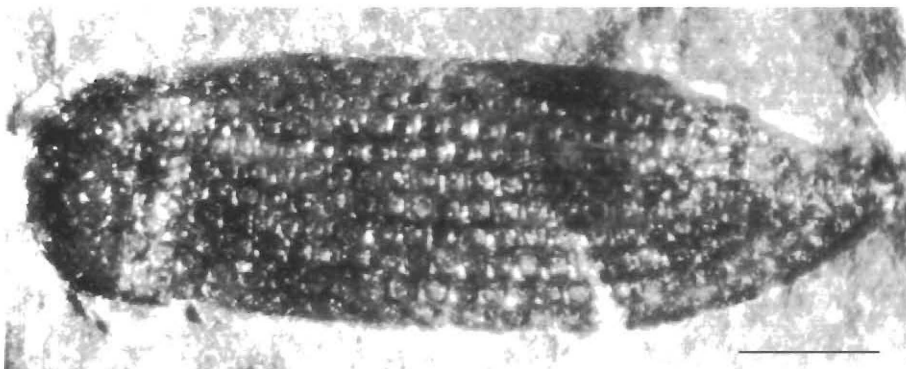


Fig. 7 - *Notocupes* sp. (MCSN 5002). Scale bar: 1 mm.

Order Coleoptera Linné 1758 Family Cupedidae Lacordaire 1857

Beetles (Coleoptera) are known since the Lower Permian (Kukalová 1965). Presently this group is the most speciose insect order (ca. 350, 000) and inhabits a

diverse spectrum of environment. They are frequently recorded from the Late Triassic of Europe; however, most occurrences are isolated elytrae that disallow more precise taxonomic assignments. Complete specimens are extremely rare.

The principal information regarding the Triassic

representatives of Cupedidae is found in Ponomarenko (1969). This extant family is known since the Lower Triassic, during which it consisted of three subfamilies with numerous species. The Triadocupedinae are recorded only from the Triassic, while Ommatinae and Cupedinae are still extant.

The specimen found in Meride belongs to the extinct genus, *Notocupes* Ponomarenko, of the Ommatinae. Recent representatives of this subfamily have a Palaearctic distribution and live in decaying wood (Fukuda 1941).

Genus *Notocupes* Ponomarenko, 1964

Notocupes sp.

Material: one specimen (MCSN 5002) from Middle Triassic, Meride (Canton Ticino, Switzerland). Stored in Museo Cantonale di Storia Naturale, Lugano (Switzerland).

Description. A single elytron preserved (Fig. 7), 6.5 mm long and 2.0 mm wide, with well preserved venation

and rows of punctures. Identifiable features of the venation are present to allow assignment of this specimen to the genus; however, the specific assignment is not possible on the basis of a single elytron.

The genus is known from ca. 50 species from the Upper Triassic (Carnian) to the Paleocene (Ponomarenko, personal communication).

Acknowledgements.

We are greatly obliged to the scientists of the Laboratory of the Fossil Insects (Palaeontological Institute, Russian Academy of Sciences in Moscow) for the help in identification of the specimens. Our special thanks are due to Dr. N. Sinichenkova, Prof. A. Ponomarenko and Prof. A. Rastnitsyn.

The field work has been supported by grants from the Land Departments of the Canton Ticino and the Federal Office for Environment, Forests and Landscape in Berna to the Museo Cantonale di Storia Naturale in Lugano. A special thanks goes to Dr. M. Felber, curator for geology at the Lugano Museum, for his continuous support. Dr. H. Wilson and Dr. C. Labandeira did the critical reading: to them our warm thanks for their suggestions greatly improved the paper.

REFERENCES

- Bassani F. (1886) - Sui fossili e sull'età degli schisti bituminosi triasici di Besano in Lombardia. *Atti Soc. It. Sci. Nat.*, 29: 15-72, Milano.
- Bechly G. (1997) - New fossil odonates from the Upper Triassic of Italy, with a redescription of *Italophlebia gervasutii* Whaley, and a reclassification of Triassic dragonflies. *Riv. Mus. Civ. Sc. Nat. "E. Caffi."* Bergamo, 19: 31-70, Bergamo.
- Brauckmann C. & Schlüter T. (1993) - Neue Insekten aus der Trias von Unter-Franken. *Geologia et Palaeontologica*, 27: 181-199, Marburg.
- Bürgin T. (1992) - Basal Ray-finned Fishes (Osteichthyes, Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland). *Schweiz. Paläont. Abh.*, 114: 1-164, Basel.
- Bürgin T. (1995) - Actinopterygian fishes (Osteichthyes, Actinopterygii) from the Kalkschieferzone (Uppermost Ladinian) near Meride (Canton Tessin, Southern Switzerland). *Eclogae geol. Helv.*, 88: 803-826, Basel.
- Bürgin T. (1998) - Pesci fossili del Triassico Medio del Monte San Giorgio (Svizzera Meridionale) e della zona di Besano (Italia Settentrionale). *Geol. Insubr.*, 3: 1-9, Lugano.
- Bürgin T., Rieppel O., Sander P.M. & Tschanz K. (1989) - The fossils of Monte San Giorgio. *Sci. Amer.*, 260: 74-81, New York.
- Calafat F. (1988) - Estatigrafia y sedimentologia de la litofacies Buntsandstein de Mallorca. Tesis de licenciatura, Univ. Barcelona, 126 pp., Barcelona - unpublished.
- Carpenter F.M. (1992) - Superclass Hexapoda. In: R.C. Moore (Founder) & R.L. Kasler (ed.) - Treatise on Invertebrate Paleontology, Part R, Arthropoda 4. *Boulder (Colorado) & Lawrence (Kansas) (The University of Kansas & The Geological Society of America)*, 3-4, XXII, 655 pp., Boulder, Col. & Lawrence, Kansas.
- De Alessandri G. (1910) - Studi sui pesci triasici della Lombardia. *Mem. Soc. It. Sc. Nat.*, 3: 1-145, Milano.
- Ellenberger F., Ellenberger P., Laurentiaux D. & Ricour J. (1952) - Note préliminaire sur la faune et un niveau insectifère des lentilles de grès et schistes noirs des gypses de la Vanoise (Trias supérieur). *Bull. Soc. géol. France*, 6: 269-274, Paris.
- Fliche P. (1901) - Sur un insecte fossile trouvé dans le Trias en Lorraine. *C. R. hebdomadaire des séances Académie des Sciences*, 132: 650-651, Paris.
- Fukuda A. (1941) - Some ecological studies on *Cupes clathratus* Salsky from Japan. *Trans. Nat. Hist. Soc. Formosa*, 31 (217/218): 394-399 [in Japanese with English summary], Taiwan.
- Furrer H. (1995) - The Kalkschieferzone (Upper Meride Limestone; Ladinian) near Meride (Canton Ticino, Southern Switzerland) and the evolution of a Middle Triassic intraplateau basin. *Eclogae geol. Helv.*, 88: 827-852, Basel.
- Geyer G. & Kelber K.P. (1987) - Flügelreste und Lebensspuren von Insekten aus dem Unteren Keuper Mainfrankens. *N. Jb. Geol. Paläont. Abh.*, 174: 331-355, Stuttgart.
- Grauvogel L. & Laurentiaux D. (1952) - Un Protodonate du Trias des Vosges. *Ann. Paléontologie*, 38: 121-129, Paris.
- Handlirsch A. (1918) - Fossile Ephemeridenlarven aus dem Buntsandstein der Vogesen. *Verh. zool. botan. Gesell. Wien*, 68: 112-114, Wien.

- Heer O. (1864) - Über die fossilen Kakerlaken. *Vierteljahrsschrift der naturforschenden Gesellschaft Zürich*, 9 (4): 273-302, Zürich.
- Hubbard M.D. & Riek E.F. (1977) - New name for a Triassic mayfly from South Africa (Ephemeroptera). *Psyche*, 83: 260-261, Cambridge, Mass.
- Hyatt A. & Arms J.M. (1890) - Guides for Science Teaching, n°8: *Insecta*. V. of 300 pp., Paris.
- Kinzelbach R. (1970) - Eine fossile Eintagsfliege aus dem Perm des Saar-Nahe-Pfalz-Gebietes (Ephemeroptera: Permoplectoptera: Misthodotidae (Tillyard 1932). *Mainzer naturw. Arch.*, 9: 318-322, Mainz.
- Kinzelbach R. und Lutz H. (1984) - Eine neue Eintagsfliege *Misthodotes stapfi* n. sp. aus dem Rotliegenden des Nahe-Gebietes (Ephemeroptera: Permoplectoptera: Misthodotidae). *Paläont. Z.*, 58 (3/4): 247-253, Stuttgart.
- Krzeminski W. & Jarzembowski E. (1999) - *Aenne triassica* sp. n., the oldest representative of the family Chironomidae (Insecta: Diptera). *Polskie Pismo Entomologiczne*, 68: 445-449, Wrocław.
- Krzeminski W. & Krzeminska E. (1996) - Revision of Laurentiptera gallica from the Lower/Middle Triassic of France (Mecoptera: Liassophilidae). *Polskie Pismo Entomologiczne*, 65: 267-274, Wrocław.
- Krzeminski W., Krzeminska E. & Papier F. (1994) - *Grawvogelia arzuilleriana* n. gen., n. sp. the oldest Diptera species (Lower/Middle Triassic of France). *Acta zoologica cracoviensia*, 37(2): 95-99, Kraków.
- Kühn O. (1838) - Neue Insektenreste aus der deutschen Lettenkohle (Obertrias). *Beiträge zur Geologie von Thüringen*, 5 (2): 84-86, Leipzig.
- Kuhn-Schnyder E. (1974) - Die Triasfauna der Tessiner Kalkalpen. *Njbl. natf. Ges. Zürich*, 176: 19, Zürich.
- Kuhn-Schnyder E. (1987) - Die Triasfauna der Tessiner Kalkalpen XXVI. *Lariosaurus lavizzarii* n. sp. (Reptilia, Sauropterygia). *Schweiz. Paläont. Abh.*, 110: 1-24, Basel.
- Kukalová J. (1965) - Permian Protelytroptera, Coleoptera and Prothoptera (Insecta) of Moravia, *Sborník Geologických Ved*, 6: 61-98, Warsaw.
- Kukalová J. (1968) - Permian mayfly nymphs. *Psyche*, 75: 320-327, Lexington/Mass.
- Kukalová-Peck J. (1985) - Ephemeroid wing venation based upon new Carboniferous mayflies and basic morphology, phylogeny and metamorphosis of pterygote insects (Insecta, Ephemera). *Canadian Journ. of Zoology*, 63: 933-955, Ottawa.
- Lacordaire J. T. (1857) - Histoire naturelle des Insectes. *Genre des Coléoptères*, part 4. Roret. V. of 579 pp., Paris.
- Laurentiaux D. (1953) - Classe des Insectes, III: 397-527, In: Piveteau J. *Traité de Paléontologie*. Masson and Cie, Paris.
- Lombardo C. (1997) - Ittiofauna della Kalkschieferzone (Calcarea di Meride, Ladinico Superiore) di Ca' del Frate (Viggiù-Varese). Tesi di dottorato, Università degli Studi di Milano, 1997.
- Lombardo C. (1999) - Sexual dimorphism in a new species of the actinopterygian *Peltopleurus* from the Triassic of Northern Italy. *Palaeontology*, 42: 741-760, London.
- Lombardo C., Tintori A., Felber M., Danini G., Moratto D., Pacor G. & Tentor M. (1998) - Nota preliminare sul primo ritrovamento di un insetto fossile nell'area di Monte San Giorgio (Canton Ticino, Svizzera), *Geologia Insubrica*, 3: 33-34, Lugano.
- Lombardo C., Tintori A., Felber M., Danini G., Moratto D., Pacor G. & Tentor M. (1999) - Faunal assemblages in the Kalkschieferzone (Meride Limestone, Upper Ladinian) of Meride (Canton Ticino, Switzerland). Abstract in: Third International Symposium on Lithographic Limestones, in: *Riv. Mus. Civ. Sc. Nat. "E. Caffi."* Bergamo, suppl. v. 20: 101-104, Bergamo.
- Marchal-Papier F. (1998) - Les insectes du Buntsandstein des Vosges (NE de la France). Biodiversité et contribution aux modalités de la crise biologique du Perm-Trias. These pour obtenir le grade de Docteur de l'Université Louis Pasteur de Strasbourg. 168 pp. - unpublished.
- Meunier F. (1907) - Un Odonatoptère du Rhétien de Fort-Mouchard près des Arçures. *Bull. Muséum Hist. natur. Paris*, 7: 521-522, Paris.
- Nel A. (1989) - *Piroutetia liasina* Meunier, 1907, Insecte du Lias de France, espèce-type des *Piroutetiidae* nov. fam. *Bull. Muséum nat. Hist. nat. Paris*, 4 (11) C, 1:15-19, Paris.
- Papier F. & Grauvogel-Stamm L. (1995) - Les Blattodea du Trias (Anisien) des Vosges (France): le genre *Voltziabatta* n. gen. du Grès a Voltzia (Buntsandstein supérieur). Morphologie, systematique et affinités. *Palaeontographica A*, 235 (4-6): 141-162, Stuttgart.
- Papier F., Nel A. & Grauvogel-Stamm L. (1996) - Deux nouveaux insectes Mecopteroidea du Buntsandstein supérieur (Trias) des Vosges (France). *Paleontologia Lombarda* (N.S.), 5: 37-45, Milano.
- Papier F., Grauvogel-Stamm L. & Gall J.C. (1997) - La plus ancienne sauterelle Tetigoniidae (Trias, NE France): mimetisme ou exaptation? *Paläont. Z.*, 71 (1/2): 71-77, Stuttgart.
- Ponomarenko A.G. (1964) - Novye zhuki semeystva Cupedidae iz yurskikh otlozhenij karatau [New beetles of the family Cupedidae from the Jurassic deposits in Karatau]. *Paleont. zhurnal*, 1964 (2): 49-62, Moskov.
- Ponomarenko A.G. (1969) - Historical development of Coleoptera-Archostemata. Trudy PIN AN SSSR, 125: 3-239, Moscov - (in Russian).
- Ponomarenko A.G. & Sukatcheva I.D. (1998) - Nasekomye. In: Granitza Permi i Triasa v kontinentalnykh seeakh vos-tochnoi Evropy. GEOS: 96-106, Moscov - (in Russian).
- Reposi E. (1909) - Gli scisti bituminosi di Meride e Besano e la loro industria. Tipografia C. Traversa, Lugano-Mendrisio.
- Renesto S. (1993) - A juvenile *Lariosaurus* (Reptilia, Sauropterygia) from the Kalkschieferzone (Uppermost Ladinian) near Viggiù, (Varese, Northern Italy). *Riv. It. Paleont. Strat.* 99: 199-212, Milano.
- Riek E. F. (1976) - An unusual mayfly (Insecta: Ephemeroptera) from the Triassic of South Africa. *Palaeont. Afr.*, 19: 149-151, Johannesburg.
- Roemer F. (1876) - Notiz über ein Vorkommen von fossilen Käfern (Coleoptera) im Rhät bei Hildesheim. *Z. deutsch. geol. Ges.* 28: 350-353, Stuttgart.

- Sandberger F. (1867) - Bemerkungen über einige Versteinerungen aus Wellenkalk und Lettenkhöle. *Würzburger naturw. Zeitschr.*, 6: 131-208, Würzburg.
- Sander P. M. (1989) - The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the description of new species. *Phil. Trans. R. Soc. Lond. B*, 325: 561-670, London.
- Scheuring B. W. (1978) - Mikrofloren aus den Meridekalken des M.te San Giorgio (Kanton Tessin). *Schweiz. Paläont. Abh.*, 100: 1-100, Basel.
- Stoppani A. (1857) - Studii geologici e paleontologici sulla Lombardia. Turati, Milano.
- Tchernova O. A. (1965) - Some fossil mayflies (Ephemeroptera, Mithodotidae) from Permian-beds of the Ural. *Rev. Ent. USSR*, 44 (2): 253-361, Moscow.
- Teixeira C. (1947) - Nota sobre um Blatido fossil do Retiano de Coimbra. *Bol. Soc. Geol. Portugal*, 6: 243-244, Lisboa.
- Teruzzi G. & Dal Sasso C. (1995) - Recent research in the Besano Fm., Middle Triassic, Northern Italy. *Europal, Newsletter*, III EPA Workshop: Black shales models, Dotternhausen, July, 6-8 1995: 74-75.
- Thompson D.B. (1965) - The occurrence of an insect wing and branchiopods (Euestheria) in the Lower Keuper Marl at Styal, Cheshire. *The Mercian Geol. Journ. East Midlands Geol. Soc.*, 1: 237-245, Nottingham.
- Tillyard R.J. (1932) - Kansas Permian insects. Part. 15. The order Plecoptera. *Am. J. Sci.*, 5 (23): 98-134, 237-272, New Haven/Conn.
- Tintori A. (1990a) - Estherids from the Kalkschieferzone (Triassic) of Lombardy (N. Italy). In Robba E. (ed.): *Atti 4° Simposio Ecol. Paleoc. Comunità Bentoniche* (1988): 95-105, Torino.
- Tintori A. (1990b) - The actinopterygian fish *Prohalecites* from the Triassic of Northern Italy. *Palaeontology*, 33: 155-174, London.
- Tintori A. & Lombardo C. (1999) - Late Ladinian fish faunas from Lombardy (N-Italy): stratigraphy and paleoenvironment. *Proceedings of Second International Meeting on Mesozoic Fishes "Systematics and the fossil record"*. G. Arratia & H.-P. Schultze (eds.): 495-504, Verlag Dr Friedrich Pfeil, München, Germany.
- Tintori A., Lombardo C., Danini G., Felber M., Marazzi B. & Vendico M. (1998) - Scavi paleontologici nella Kalkschieferzone di Meride (Canton Ticino, Svizzera) risultati preliminari della campagna 1997. *Geologia Insubrica*, 3/1: 11-16, Lugano.
- Tintori A., Muscio G. & Nardon S. (1985) - The Triassic fossil fish localities in Italy. *Riv. It. Paleont. Strat.* 91: 197-210, Milano.
- Tintori A. & Renesto S. (1983) - The Macrosemiidae (Pisces Actinopterygii) from the Upper Triassic of Lombardy. *Riv. It. Paleont. Strat.* 89: 209-222, Milano.
- Tintori A. & Renesto S. (1990) - A new *Lariosaurus* from the Kalkschieferzone (Uppermost Ladinian) of Valceresio (Varese, N. Italy). *Boll. Soc. Pal. It.*, 29: 309-319, Modena.
- Via L. & Calzada S. (1987) - Arthropodos fosiles Triasicos de Alcover-Montral I. Insectos. *Cuad. Geologia Iberica* 11: 273-280, Madrid.
- Whalley P. (1986) - Insects from the Italian Upper Trias. *Riv. Mus. Civ. Sc. Nat. "E. Caffi."* Bergamo, 10: 51-60, Bergamo.
- Wirz A. (1945) - Beiträge zur Kenntnis des Ladinikums in Gebiete des Monte San Giorgio. Die Triasfauna de Tessiner Kalkalpen XV. *Schweiz. Pal. Abh.* 65: 1-84, Zürich.
- Zeuner F.E. (1930) - Über einige Käfer aus dem deutschen Keuper. *Jahrb. preuss. geolog. Landesanstalt*, 51: 462-467, Berlin.