UNIVERSITÀ DEGLI STUDI DI MILANO

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THE TRIASSIC INSECTS FROM MONTE SAN GIORGIO: SYSTEMATICS AND PALEOENVIRONMENTAL IMPLICATIONS

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Sommario

1. *Introduzione*

Monte San Giorgio (MSG) is a fossil Lagerstätte known since the 19th Century thanks to the industrial exploitation of bituminous shales and to the numerous paleontological excavations that took place mainly in the last century. In time, it has yielded several remarkable fossils of marine fishes and reptiles as well as invertebrates, namely crustaceans and insects and plant remains. Lying across the Italian-Swiss boundary to the South of the Ceresio Lake (Fig. 1), this area is now in the World Heritage List of UNESCO for the global paleontological meaning of its marine vertebrate faunas.

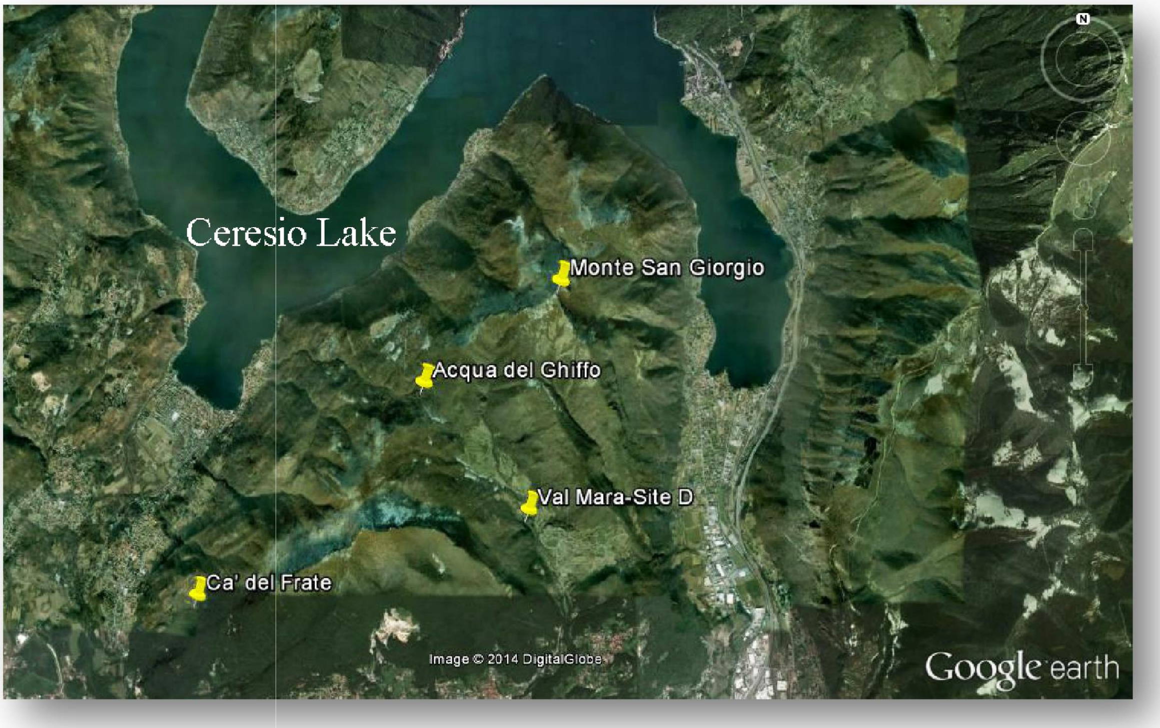

Fig 1: Val Mara site D - geographic position

During the fieldwork carried out between 1997 and 2003 in the Lower Kalkschieferzone (KSZ) at the Val Mara site D near Meride (Canton Ticino, Svizzera), 16 specimens of insects (both adult and larval forms) were collected by the UNIMI team lead by Prof. A. Tintori and Dr. C. Lombardo and with the support by Dr. Markus Felber,then curator at the Museo Cantonale di S.N. in Lugano (MCSN). At the time this PhD project started, only four of them had been described: three as a new genus and species of Ephemeroptera, *Tintorina meridensis* Krzeminski & Lombardo, 2001 and the other as an elytron of *Notocupes* (Coleoptera: Ommatidae) (Krzeminski & Lombardo, 2001).

After this first approach, the fossil insects collection of Monte San Giorgio kept at the Dipartimento di Scienze della Terra'A. Desio' of the Università degli Studi of Milano on behalf of the MCSN, were set aside as only the vertebrate fauna from the same fossiliferous level, the Kalkschieferzone, was further investigated.

In 2011, Bechley and Stockar (2011) described three specimens of *Dasyleptus triassicus* (Archaeognatha: †Monura: †Dasileptidae) collected during a small size excavation carried out by the MCSN in 2010 in site VM 227 of the Kalkschieferzone. Furthermore, two more insects from the same level, a beetle and a dragonfly, are currently under studyin Lugano.

Thus, the increasing number of fossil insects records from the KSZ brought new attention to the topic with a dedicated PhD project.

The PhD projects started with a double aim:

- to study and describe the remaining insect specimens from the KSZ;
- to increase the information on the Monte San Giorgio paleoenvironment on the basis of the fossils possible living habits, inferred from those of extant closer relatives, and from their way of preservation.

In process, the Middle Triassic entomofauna from Monte San Giorgio has proved to be even more interesting than previously supposed.

From the systematic and evolutionary point of view, it's a very diverse assemblage and it includes the oldest fossil record so far known for four taxonomic groups.

Even more exceptional is the conservational aspect: part of the specimens underwent soft-tissue phosphatization, that preserved unique anatomical features normally lost in fossil insects/arthropods. The preservation of such soft tissue structures points to unique fossilization conditions that is unknown for the vertebrates yielded by the same MSG beds. Analogous preservations are known only from the Cambrian fauna of Chengjang in China.

Thus, the paleoenvironmental indications that could potentially be derived from the composition and taphonomic history of this entomofauna are getting into light.

2. *Insects in the Triassic*

The Triassic entomofaunas are of particular interest, since they are the product of the recovery following the end-Permian mass extinction event and can therefore provide information about the real impact of the end-Permian life crisis on the insects as on the possible radiation following the extinction of old taxa.

An overview of insects through time is provided by Grimaldi and Engel (2005) and by Rasnitsyn and Quicke (2002). The evolution of Permian and Mesozoic Coleoptera is described in Ponomarenko (1995).The best picture of the earliest known Triassic insect fauna can be drawn by the assemblage from Grès a Voltzia, Early Anisian, 247-245Ma (Gall and Grauvogel-Stamm, 2005; Bethoux et al., 2005).

Despite the paucity of the Triassic insects sites, the assemblages recovered appear to be quite diverse, particularly if compared to vertebrate ones. Terrestrial and aquatic, predatory and phytophagous forms are preserved, an indication that virtually all the niches were available and exploited.

Many of the most primitive taxa disappeared (from the fossil record so far available) at the end of the Permian. The most remarkable among them is the superorder Paleodyctiopterida, with its huge fossils with beautifully patterned wings. Also a few stem groups to modern orders didn’t survive the P/T boundary event.

The Triassic fossil record unfortunately suffers from a gap in the Lower Triassic rocks. The fossil record currently available could indicate that the end-Permian event wiped out a few Paleozoic groups but many insect orders seems to have survived the P/T boundary, then further radiating in the Triassic: Odonata, Plecoptera, Ephemeroptera, Coleoptera and Diptera, developed successful lineages, many of them still extant.

Moreover, new discoveries can often complicate the reference frame: recently Bechly and Stockar (2011) identified three specimens of a new species *Dasylepus triassicus* (Archaeognatha: † Monura) from the Upper Kalkschieferzone of Monte San Giorgio, site VM 227, thereby extending the range of this genus for 10 My from the end of Permian into the Mesozoic, when accepting the revision of *Triassomachilis uralensis* Sharov, 1948 and its reassignment to Ephemeroptera (Sinitshenkova, 2000). In fact, the most recent Monuran before *D. triassicus* is *Dasyleptus brongniarti* Sharov 1957 from the Upper Permian of Russia (circa 270-252 Ma). This finding stresses the role played by the incompleteness of the fossil record in biasing hypothesis on taxa evolution.

Typical Paleozoic forms are occasionally recovered until the Middle Jurassic. For instance, Glosselytrodea have been found in virtually all the Triassic sites: the Röt-Formation (Bashkuev et al., 2012), the Los Rastros formation (Mancuso et al, 2007), the Madygen Formation (Shcherbakov, 2008) and the Molteno Formation (Anderson et al., 1998); Miomoptera are in the Madygen Formation and in the Los Rastros Formation and Titanoptera in the Madygen Formation.

Concerning extant orders, at first sight most of them can be found in the Triassic fossil record, with the notable exception of Lepidoptera. Anyway, a closer examination shows that many representatives of the major lineages were stem groups or sister groups of the extant forms that lately became extinct.

A few examples are clearly outlined by Gall and Grauvogel-Stamm (2005) from Grès a Voltzia, the oldest Triassic insect site and therefore the closest to the P/T boundary, dated early Anisian. They refer to Blattoptera, Odonatoptera and Ephemeroptera, that are among the more abundant taxa there recovered.

Blattoptera are represented by genera exhibiting Paleozoic characteristics and by genera similar to modern ones, as *Voltziablatta* and *Scleroblatta*. Odonatoptera arepresent with *Voltzialestes* (Protozygoptera), announcing modern Odonata, and with a representative of the Paleozoic family Triadotypidae. Finally, a mayfly isolated wing shows affinities with a Permian family, while a larva is similar to those of the extant family Siphlonouridae.

Modern Blattodea and Ephemeroptera probably originated in the Jurassic and were first recovered as fossils from the Early Cretaceous. Modern Odonata were evolving in the Triassic.

Coleoptera made their first appearance in the Permian with ancient forms, but true Coleoptera appeared in the Triassic. Ponomarenko (1995) identifies two main stages in the evolution of Coleoptera: the first stage involves the Triassic and the first half of the Jurassic; the second one the Upper Jurassic and the Early Cretaceous. Permian beetles were mainly xylomycetophagous and detritophagous Cupedoid and Schizophoroid, with the exception of few predaceous specimens. In Triassic sites, Archostemata are still abundant, but Adephaga and Polyphaga become more numerous. In the Early Jurassic, Archostemata are no longer the more abundant group and adephagan beetles become dominant, in particular with Trachypachidae, now a relict group, and Carabidae. Adephagan aquatic forms are also recovered († Coptoclavidae, † Parahygrobiidae, Liadytidae, Gyrinidae, Hydrophilidae) both as adults and as larvae. Finally, in the Late Jurassic, beetle assemblages more closely resemble modern ones: polyphagan become dominant with several families, and carnivorous, predaceous taxa increase among Adephaga (Carabidae).

Extant orders already established in the Triassic include Hemiptera, Orthoptera (Ensifera), Odonata, Plecoptera, Dermaptera, Phasmatodea, Coleoptera, Diptera. A Triassic origin is also hypothesized for: Embiodea and Zoraptera, two strictly related taxa.

3. *Triassic insect sites*

Triassic insect sites are not abundant. On the other side, the few renowned sites yield hundreds or even thousands of specimens, whole or partially preserved.

The more significant Triassic insect sites are:

- Grès a Voltzia (Anisian), in the Vosges Mountains (France).
- Many areas in Central Asia, as Kazakhstan, Uzbekistan, Kyrgyzstan. Among Central Asia sites by far the most important one is the Madygen Formation, dated Late Ladinian – Early Carnian (236-230 Ma), located in the Fergana valley (split among Uzbekistan, Kyrgyzstan, Tajikistan).
- Molteno Formation, part of the Karoo Group, South Africa, dated Carnian.
- Potrerillos and Los Rastros Formation in Argentina, dated Carnian or Ladinian-Carnian.

Interesting sites can also be found in the area surrounding Sydney in Australia, dated Anisian or Upper Triassic/Lower Jurassic.

In the following sections a description of Grès a Voltzia, Madygen, the Los Rastros and the Molteno Formations is provided. They altogether span from the Anisian and the Carnian stages.

3.1. Grès a Voltzia

The Grès à Voltzia Formation (Upper Buntsandstein) is located in eastern France (Fig.2). It is Early Anisian in age and it spans the transition from the continental formations of the Buntsandstein to the marine sedimentation of the Muschelkalk. It was deposited on the western margin of the Germanic Basin, a broad depression extending over a large part of Central Europe and including a great part of Germany (Shear et al, 2009).

Since it's been deposited approximately eight My after the Permian–Triassic boundary, according to the biostratigraphic correlations between the Germanic Buntsandstein and the Alpine Triassic units, it is of particular interest for the information it provides on the very early stage of recovery from the Permo-Triassic event.

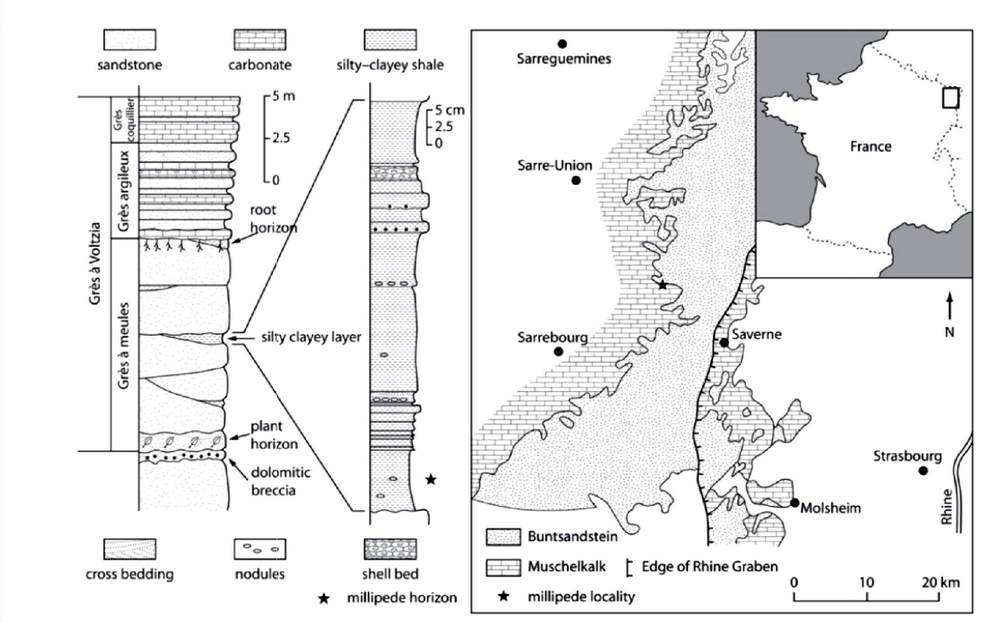

Fig. 2 Grès à Voltzia Formation location and stratigraphic structures. From Shear et al., 2009

It was deposited in a deltaic area, an environment transitional from nearshore to terrestrial, in a fluvial environment that included a network of channels and overbank flats.

The most important layer is called 'Grès à meules' that forms the lower level of the Grès à Voltzia Formation.

Three facies have been recognized in the Grès à meules Formation (Gall 1983, 1985):

a) thick lenses of fine-grained sandstone, grey or pink but most often multicoloured, containing land plant debris and stegocephalian bone fragments;
b) green or red silt/clay lenses, generally composed of a succession of laminae each a few millimeters thick, with well preserved fossils of aquatic and terrestrial organisms;
c) beds of calcareous sandstone with a sparse marine fauna.

The three units are interpreted as follows: the sandstone facies corresponds to point bars deposited in meandering channels; the clay lenses represent the settling of fine material in brackish ponds; the calcareous sandstone results from brief incursions of sea water during storms.

Insects have been collected from the clay lenses, together with other terrestrial invertebrates (spiders, terrestrial scorpions) and aquatic fauna including medusoids, annelids, *Lingula*, bivalves, limulids, crustaceans. Some animals (e.g. *Lingula*, bivalves) are preserved in life position. Many arthropods (limulids, crustaceans) show, in the same horizon, different larval stages, adults, and moults/exuviae. Clutches of insect eggs, coprolites, and trace fossils are also present. All these elements point to an autochthonous origin of this fauna. Characteristically, the biota is rich in individuals but poor in species (Gall 1983, 1985), with the exception of arthropods: 18 species of crustaceans and about 200 species of insects have been collected.

The site was located in the subtropics near the eastern edge of Pangaea and this, together with the red-beds and the xeromorphic land flora (Gall 1983), suggest it was subject to a semi-arid climate. On the other hand, the deltaic situation suggests that aridity was not severe locally, possibly thanks to a seasonal climate. In fact, clay lenses deposited when pools formed during the wet season evaporated as the dry season approached. The presence of *Lingula* in situ, together with the impoverished species diversity, strongly suggests a brackish water community (Gall 1983): probably, from time to time, the delta area was briefly invaded by the sea during storms. Land plants are abundant and mark the proximity of stable emerged land. The floral assembly includes horsetails, ferns, and gymnosperms (‘*Voltzia*’)

On the basis of this evidence Gall (1983) concluded that the aquatic fauna was autochthonous and that the preserved terrestrial fossils accidentally reached the site of burial from the adjacent terrestrial environment. For instance, during flooding, the plants and the amphibians living on land were dragged and dropped downstream.

The preservation of the fossils is remarkable, as it includes both mineralized tissues and soft-bodied organisms.

Among the insects, the dominant groups are Blattodea (41%), Ephemeroptera (15%) and Coleoptera (12%). Representatives of 12 orders were identified by 2005 (Gall and Grauvogel-Stamm), with the highest number of species among Ephemeroptera, Diptera, Orthoptera and Blattodea.

3.2. Madygen

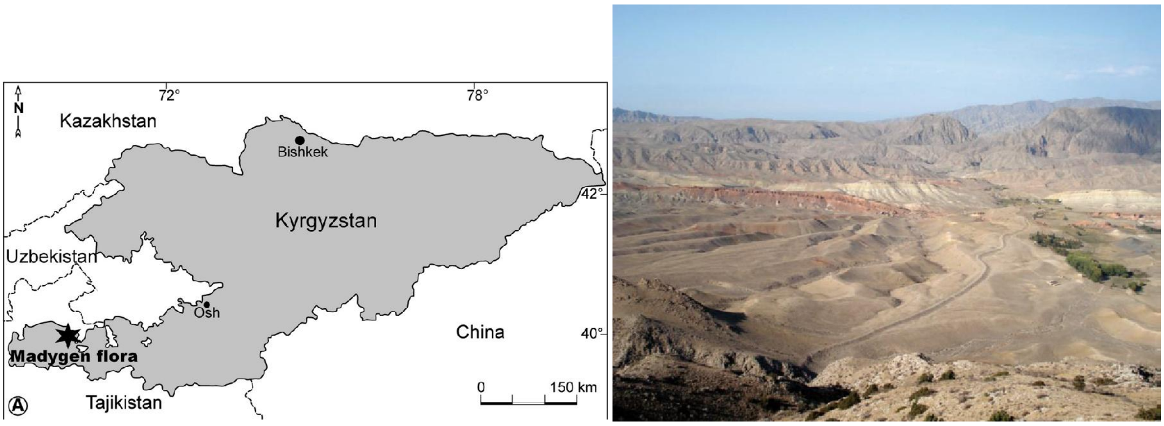

Fig 3 – A: map of Central Asia showing the location of the Madygen Formation in SW Kyrgyzstan. From Moisan et al, 2011; B: Madygen outcrops, from Shcherbakov (2008).

The Madygen site is named after the village of Madygen, in the foothills of the Turkestan Range, Kyrgyzstan. It is a formation cropping out in five adjacent areas, over an extension of approximately10 km2.

It is a continental, tectonically active basin flanked by ranges of Palaeozoic rocks. In its stratotype area the Madygen Formation consists of an approximately 560 m thick succession of complexly interbedded conglomerates, sandstones and siltstones, generally representing deposits of alluvial fans, alluvial plains, and lakes.

The predominantly reddish-brown to yellowish-green coloured coarse-clastic fan deposits are almost bare of fossils. Alluvial plain deposits are more heterogeneous, consisting of poorly sorted conglomeratic to sandy channel fills, mudflow, and silty overbank deposits. These rocks are locally rich in fossils. The richest and most diverse fossil associations, however, occur in laminated to massive brownish-grey lacustrine siltstones.

From the relative abundance of root traces in silty overbank deposits, the high content of organic carbon, the presence of coal beds and the lack of desiccation cracks, it was concluded that alluvial plains, delta plains, and shallow lacustrine environments of the Madygen Formation were densely vegetated wetland areas (Voigt et al., 2007; Berner et al., 2009; Buchwitz et al., 2009).

The richest area in insects in the Madygen Formationin it’s Dzhailoucho, in the northern outcrop area. Shcherbakov, who has intensively investigated the insect fossil assemblage from the site, considers Dzhailoucho the richest fossil insect site in the world in terms of diversity and especially of abundance.

Fossils are preserved in a clayey matrix, poorly lithified, that dissolves after heavy rains. Terrestrial plants are common and include pteridosperms, conifers, ferns, horsetails, lycopsids, thallophytes.

Sixtel (1960) believes Dzhailoucho beds were left by a shrinking, mineralized oxbow lake formed by the Madygen River in its flow towards northwest. The paleoclimate was reconstructed as seasonal and arid, and the landscape as an intermontane river valley.

The Dzhailoucho lake water was highly mineralized and low in oxygen (dipnoan fishes were common there). A reconstruction of the paleoenvironment depicts tall horsetails growing along the banks as emergent semiaquatic plants. Hepatics formed thick floating mats on or under the water surface, creating a microhabitat that was somewhat richer in oxygen and densely populated by diverse insects and other invertebrates

Tetrapods in the Madygen Formation are represented by *Triassurus,* interpreted as a stem-caudate or temnospondyl larva (Milner 2000), the primitive cynodont *Madysaurus* (Tatarinov 2005), and two gliding reptiles (*Sharovipteryx* and *Longisquama*).

Among aquatic species four genera of freshwater bivalves, several small floating statoblasts of freshwater bryozoans, two species of phyllopod crustaceans, some undescribed Ostracoda and Decapoda were found. Fossil fishes (Sytchevskaya, 1999) include Dipnoa, Actinopterygii (Evenkiidae, Palaeoniscidae, Perleididae, and Saurichthyidae) and elasmobranch egg capsules probably layed by hybodont sharks (Fischer et al. 2007).

The Madygen insect assemblage is numerically dominated by insects with sclerotized forewings: Coleoptera, Blattodea, and Homoptera Auchenorrhyncha. In most outcrops, few other insects are present. In Dzhailoucho, subdominants are Mecoptera, Protorthoptera s.l., and Orthoptera, with other common groups including Miomoptera, Phasmatodea and Neuroptera. Nearly all insects are flying adults; immatures are very rare and fragmentarily preserved.

Twenty insect orders (almost everyone known in the Triassic, except for Thysanoptera and Megaloptera) and nearly one hundred families have been recorded, and more than half thousand species have been described from the Madygen Formation.

Aquatic/ amphibiotic insects are less numerous than terrestrial, but it is difficult to estimate absolute abundance, because of possible bias in sampling and/or preservation:

water beetles are quite common (abundant Schizophoroidea and rare Triaplidae), and should be some groups of Neuroptera, Mecoptera, Diptera and Protorthoptera with aquatic immature. Entirely amphibiotic orders (Ephemeroptera, Odonata, Plecoptera, Trichoptera) are uncommon, and their immatures are exceptionally rare and surely allochthonous.

3.3. Lost Rastros Formation

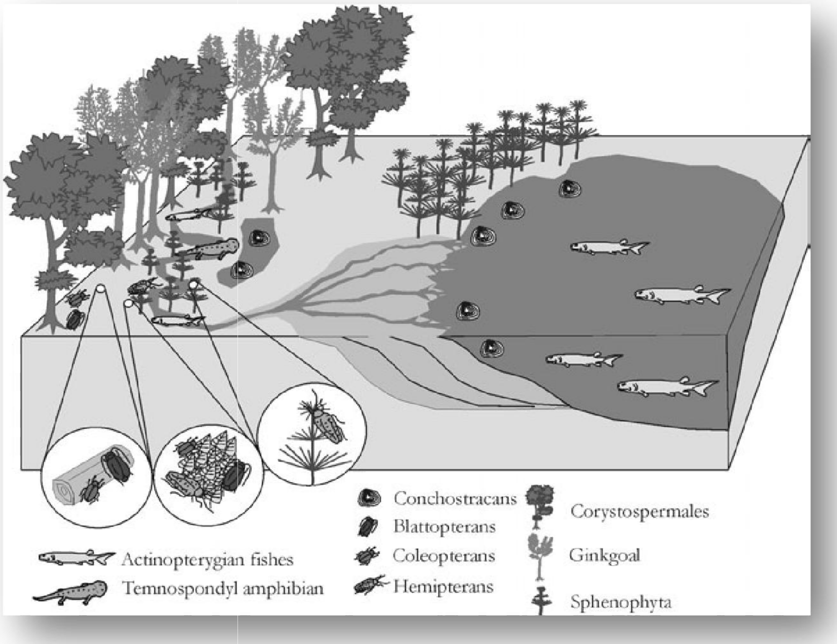

Fig 4 - Paleobiological reconstruction of the Los Rastros biota from Mancuso A.C., 2007

Los Rastros Formation belongs to the Bermejo Basin , which is an extensional basin formed along the western margin of Gondwana during the Late Permian and Early Triassic in the pre-breakup stage of Pangea (Uliana and Biddle, 1988). It is dated from the Ladinian (ca 240 Ma). Basin deposits crop out in the northwest of Argentina along the border between San Juan and La Rioja provinces, and shows a NW-SE orientation. The sedimentary infilling of the Bermejo Basin is dominated by 2.000 to 6.000 m of Triassic alluvial, fluvial and lacustrine deposits.

In the Bermejo Basin succession, including Los Rastros Formation, several lacustrine-deltaic cycles were defined, each cycle being characterized by a coarsening-upward succession, and consisting of two facies:

- Facies association A represent offshore lacustrine deposits and is dominated by claystones with iron mudstones interbedded.
- Facies association B represents deltaic deposits. The individual coarsening-upward cycle ranges, approximately, from 20 to 40 m.

Facies assemblage A, the offshore lacustrine deposit, preserves plant debris and sometimes well preserved plant fragments related to the "*Dicroidium* type Flora"; conchostracans, insects and, rarely, fish (Mancuso, 2003). The features observed in the facies assemblage A suggest that it was deposited in a deep off-shore lacustrine depositional environment.

Facies assemblage B, the delta deposits, bears fossil fish bodies and woody tissues were preserved in parallel laminated sandstones, while only fossil woods can be found in the planar and trough cross-bedded sandstones.

Besides insects, invertebrate remains include different groups of conchostracans (Mancuso et al, 2007; Mancuso and Gallego 2000), and bivalves. The vertebrate fauna is represented by skeletal remains and ichnites. The skeletal remains are dominated by actinopterygian fishes (Forster et al., 1995; Mancuso, 2003), and a single temnospondyl amphibian. The remaining tetrapod fauna is represented by non-mammalian therapsid, archosaur and possible dinosaur footprints (Arcucci et al., 1995; Marsicano et al., 2004).

The Los Rastros insect assemblage includes representatives of different orders: Blattoptera, Coleoptera, Hemiptera, Ensifera, Glosselytrodea, Odonatoptera, Miomoptera, and Plecoptera (Martins-Neto et al., 2003, 2005, 2006). Blattoptera is the most conspicuous group among the described species. The coleopteran assemblage is mainly composed by members of the suborder Archostemata (Protocoleoptera *sensu* Crowson, 1975). The Hemiptera order is represented by Cercopoidea (froghoppers, planthoppers), Dysmorphoptilidae and Scytinopteridae families (Martins-Neto et al., 2003).

The Ensifera, are one of the less common insect orders represented in the Los Rastros fossil biota, together with Miomoptera, Plecoptera and Odonatoptera (Martins-Neto et al., 2003).

The aquatic component of the Los Rastros fossil biota is very scarce, but Wilson (1988) suggests that under-representation of aquatic groups is common in the lacustrine fossil record. In the Los Rastros succession the only indirect evidence of this fact, up to date, is the record of adult forms of the orders Miomoptera, Plecoptera and Odonatoptera.

Most of the insect remains are constituted by disarticulated wings and elytra, and, only in some cases, the articulated elytra and nearly complete coleopteran bodies were found. All insect remains have been found in the laminated black shales of the offshore-lacustrine facies, and show a spatial arrangement pattern parallel to the bedding plane.

The material has been reported to be, in some cases, preserved in several successive levels, and without preferential orientation. In the insect-bearing facies, plant debris, conchostracans and isolated fish scales are also preserved. Only in seldom cases, these remains have been reported to be directly associated with insect material. All collected insect specimens are winged organisms with terrestrial habit (Gallego and Martins-Neto, 1999; Martins-Neto and Gallego, 1999, 2001; Martins-Neto et al., 2003, 2005, 2006). Thus, their origin is the shoreline of the lake or more distant areas into the affluent system.

4. Molteno Formation

The Molteno Formation, South Africa, together with the adjacent Lower Elliot Formation, forms part of the Karoo Basin and has been dated as Carnian, 228 - 235 mo (Anderson et al., 1998). It yielded a rich floral and faunal assemblages and a very diverse collection of insects. It was deposited in a northerly prograding floodplain in an extensive land-locked foreland basin, located at the southern margin of Pangea and bordered to the South by a range of possibly 4.000 m high mountains (fig. 5A).

This characteristic together with the climate and the tectonics in the period, caused cyclic rapid erosion and brought heavy sediment load to the stream beds. The climate during the deposition of the Formation was governed by the Pangea landmass, blocking both warm and cold currents and determining the onset of a belt of temperate rainfall between paleolatitudes 33°S and 66°S. In the Molteno basin a seasonal climate probably established itself, with quite arid and warm summers and wetter and colder winters. This could probably provide enough precipitation in the winter on the mountains to ensure permanent water supply to the river system.

Three primary facies are met:

1. Upward fining, coarse grained channel fill deposits;
2. Upward coarsening crevasse-splay and sheet-flood sequences;
3. Rhythmically laminated lacustrine and marsh shales deposited in the floodplain.

The Molteno Formation flora is one of the richest known Triassic floras, with 56 genera and 206 species identified. It is dominated in almost equal proportion by gymnosperms (in decreasing abundance represented by the seed fern *Dicroidium*, various ginkgophytes, conifers and cycads) and pteridophytes (in decreasing abundance taxa represented by horsetails and ferns). Mosses and liverworts are rare. Despite this high diversity, on the basis of a few dominant generas seven plant habitats have been defined, further characterized by insect assemblages

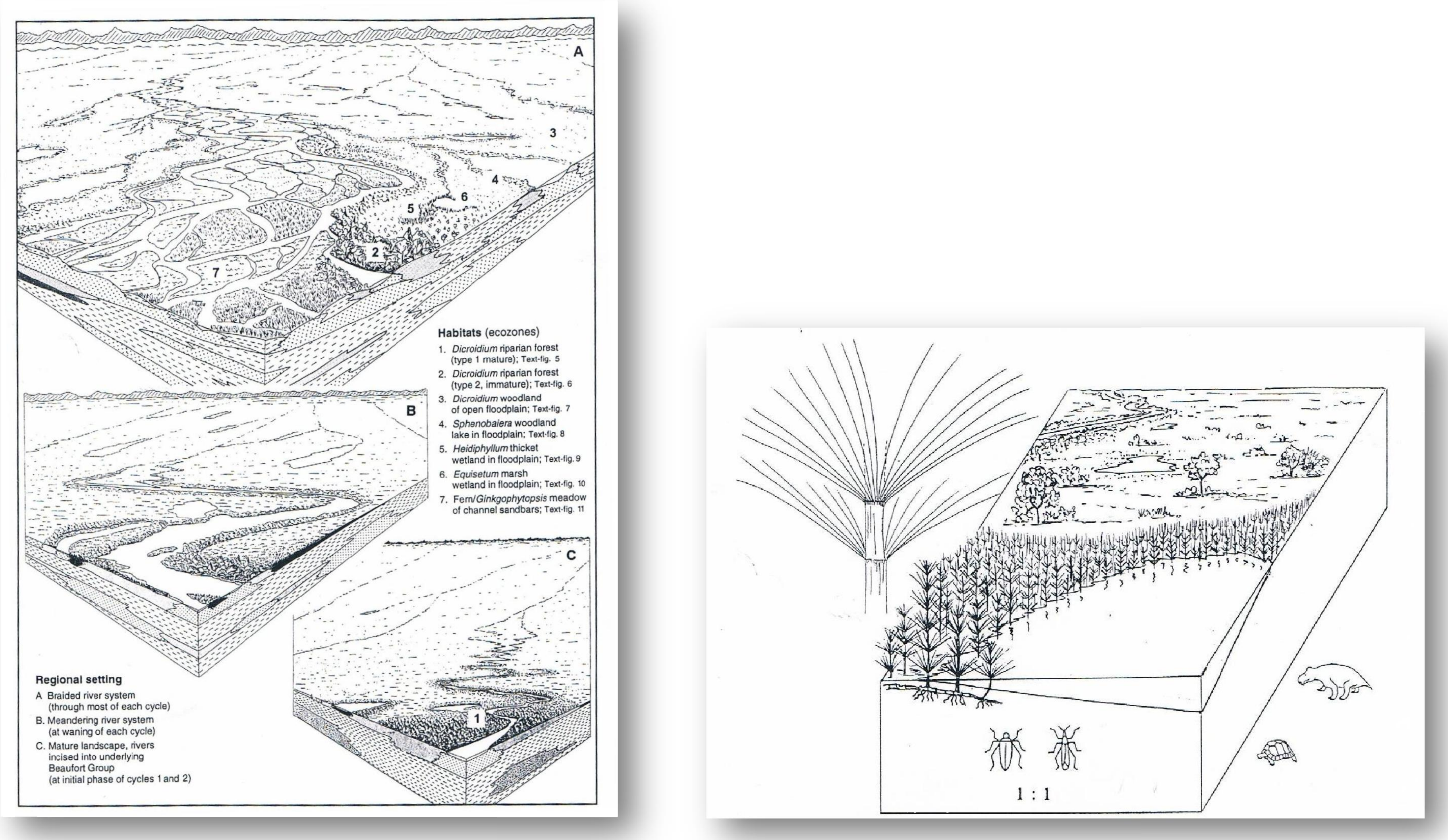

Fig 5 – **A**: regional environmental reconstruction o the molteno Biome, showing the seven habitat types or ecozones identified; B: reconstruction of Equisetum marsh in the floodplain (habitat 6), from Anderson et al. 1988

Tetrapods are preserved in the finer grained red beds and include 32 impressions of fishes, ascribed to the genus *Semionotus* and to three new genera. No tetrapod fossils have been found but trackways are reported from a single locality.

Insects have been recovered from all the levels in the Molteno Formation, albeit in some they are very rare. A clear pattern of plant/insect co-association can be recognized. In most cases, insects are preserved as isolates wings (elytra) or, more rarely, abdomens. Nymphs or larvae are more easily preserved whole, while adult insects are very rare. 18 orders, 117 genera and 335 species have been identified. Therefore, virtually all extant insect orders are present. The analyses of the depositional environment highlights the fact that most of the insects were buried in still water deposits.

Among insects, the most abundant group are Blattodea, followed by Coleoptera and Hemiptera. The most diverse one is Coleoptera, followed by Hemiptera and Odonata. The high abundance of Blattodea indicates the presence of a close-canopy terrestrial habitats where abundant leaf litter, their habitat, could form. Coleoptera are found in all the Molteno habitats. Hemiptera, are more abundant in woodland and then thicket habitats, and are rare in the riparian-forest habitats. Odonata are almost exclusively found in two habitats, namely in decreasing order of abundance: the floodplain lake deposits and the abandoned channels of the meandering river.

Among the seven habitats reconstructed based on the dominant plant species, in only one case Blattodea are not present, namely the *Equisetum* marsh in the floodplain (Habitat 6 in the work of Anderson et. al, 1998 and in fig 5 B). Here Coleoptera and Hemiptera dominate and Conchostracan are relatively common, indicating marsh conditions where leaf litter was absent.

The second most significant invertebrate (and faunal) taxa are conchostraca, with three genera and eight species.

5. *Sites comparison*

It is interesting to compare the four Triassic sites described above from the point of view of their entomofauna and of the depositional environment and paleoenvironment reconstruction.

Fist of all, of the four sites two are from Laurasia (Grès a Voltzia and Madygen) and two from Gondwana (Los Rastros Formationa and Molteno Formation).

The depositional environments in all sites was aquatic, such an environment being usually a prerequisite for fossil preservation, especially for such delicate organism as most insects are. Terrestrial habitats fail to provide the right conditions for fossilization owing to lack of continuous sedimentation.

Three of the sites, the Madygen Formation, the Molteno Formation and the Los Rastros Formation were river systems forming oxbow lakes, meanders and slow channels. Grèz a Voltzia was a riverine system subject to periodical seawater intrusions. The climate has been reconstructed as seasonal, with alternating dry and rainy seasons. The rainy season probably had monsoonal characteristics (with the exception of the Los Rastros Formation), causing periodical flooding or the formation of temporary freshwater lakes or ponds.

In the Los Rastros Formation, insects are preserved in deep off-shore lacustrine depositional environment. In the Molteno Formation, even if they are present in almost all levels with very variable abundance, the richest levels are those deposited in stillwater. In the Madygen Formation, insects are spread in all sediments. In Grès a Voltzia, the environment was a mosaic of isolated, small habitats, spread on an approximately 30 x 30 km. The presence of animals in life position (as the Brachiopod *Lingula*) and of clutches of fish and insect eggs, suggest that the main depositional environments was represented by isolated ponds harboring distinct biocenosis. These ponds underwent desiccation, causing the death of the biota and allowing its preservation.

In Grès a Voltzia insects, with at least 200 species found, are the most diverse group. Among the entomofauna, the dominant groups are Blattodea (41%), Ephemeroptera (15%) and Coleoptera (12%). Other groups include Odonatoptera, Plecoptera, Orthoptera, Phasmatodea, Hemiptera, Neuroptera, Mecoptera, Trichoptera and Diptera. The other fossils include approximately 20 species of plants and 50 species of animals, 18 of them among crustaceans.

In the Los Rastros Formation, Blattoptera is the most abundant group, while aquatic groups are very scarce and represented only by adults. The same can be said for the Madygen Formation, suggesting that these groups are underrepresented in the freshwater depositional environments that were probably their dwellings.

The abundance of Blattodea/Blattoptera is found also in the Molteno Formation (with the exception of one out of the seven plant associations identified) and in the Madygen Formation, where the group is the second most abundant following Coleoptera. They indicate the availability of abundant plant litter, that is their main food source.

From all sites, and from the Madygen Formation in particular, insect fragments are very common. Fragmentary preservation might be indicative of medium to long distance transportation, that could act as a filter in selecting more resistant parts (wings and elytra). On the other hand, the great abundance of isolated wings could be the effect of predation on insects in their living habitat.

A few features common to all Triassic sites are worth of attention:

- In all sites, insect assemblages are dominated by terrestrial forms, therefore allochthonous to the water body; aquatic groups are clearly underrepresented;
- Many specimens are preserved only as fragments, sometimes with dominance of beetles elytra, more heavily sclerotized.
- Blattodea/Blattoptera are dominant or sub-dominant.
- In all sites, with the peculiar exception of Grès a Voltzia, representatives of at least one of the Carboniferous groups has been recorded; it must be remarked that all these survivor groups disappeared before the end of the Jurassic.

The Paleozoic groups still present in the Triassic sites include (†) Paraplecoptera (Protoperlaria), (†) Meganisoptera, (†)Glosselytrodea, (†) Miomoptera and (†) Titanoptera.

(†)Glosselytrodea is an enigmatic insect order whose fossil record starts in the Permian and ends in the Upper Jurassic (Huang and Nel, 2007), included in Polyneoptera. (†)Miomoptera share the same temporal distribution and have been considered as common ancestor to all holometabolous insects. (†)Titanoptera is a Polyneopteran order recovered only from the Triassic of Australia. Paraplecoptera Martynov 1925 or Protoperlaria Tillyard 1928 is currently considered a polyphyletic group that includes a few taxa related to Plecoptera (according to Grimaldi and Engel, 2005) or to Grylloblattida (according to Rasnitsyn and Quicke, 2002) (†)Meganisoptera is a Paleozoic stem group to modern Odonata. They were giant insects, reaching a wingspan of 70 cm, The following table provides a synthesis of the entomofauna diversity in the four sites.

	Grès a Voltzia	Madygen Formation	Los Rastros Formation	Molteno Formation
Archaeognatha				x
Ephemeroptera		x		x
Odonata	x (Odonatoptera)	x	x (Odonatoptera)	x
Plecoptera	x	x	x	x
Blattodea	x	x	x (Blattoptera)	x
Mantodea				x
Orthoptera	x	x	x	x
Megaloptera				x
Neuroptera	x	x		x
Mecoptera	x	x		x
Trichoptera	x	x		x
Lepidoptera				x
Hymenoptera		x		x
Coleoptera	x	x	x	x
Phasmatodea	x	x		
Prothortoptera		x		
Dermaptera		x		
Psocoptera		x		
Diptera	x	x		
Hemiptera	x	x	x	x
Isoptera				
(†) Meganisoptera (Protodonata)				x
(†) Glosselytrodea		x	x	x
(†)Titanoptera		x		
(†) Miomoptera		x	x	
(†) Paraplecoptera				x

Tab.1: the diversity of the fossil entomofauna in four different Triassic insect sites (Grès a Voltzia, Anisian; Madygen, Ladinian-Carnian; Los Rastros Formation, Ladinian; Molteno Formation, Carnian). Odonatoptera and Blattoptera are mentioned to point out that representatives of stem groups, now extinct, of Odonata and Blattodea were found.

6. *Paleoenvironment*

The Kalkschieferzone is the uppermost member of the Meride Limestone, and is one of the fossiliferous levels of Monte San Giorgio, together with the Besano Formation (Anisian/Ladinian boundary) and the lower Meride Limestone.

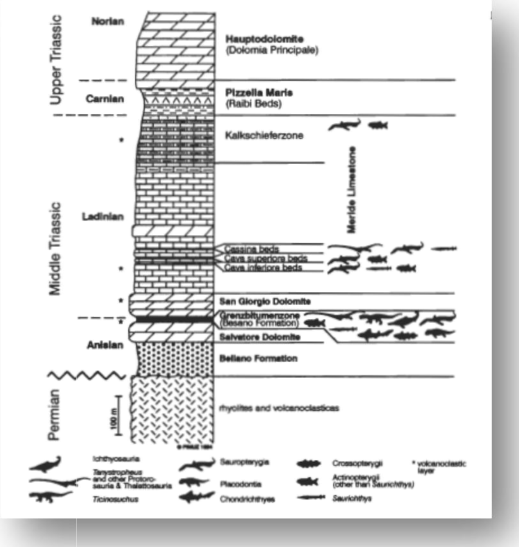

Fig 6: Stratigraphy of the Triassic sediments in the area of Monte Sang Giorgio (from Krzeminki and Lombardo, 2001)

The depositional environment of the Kalkschieferzone is that of a shallow lagoon, adjacent to a carbonatic platform (S. Salvatore Dolomite). Toward East-North/East it faces a deeper basin (Perledo-Varenna Formation) and the complex system of carbonatic platforms of the Esino Formation further to the East (Grigna Mountain), with somewhat limited connection to the open and deeper sea (Tintori 1990; Tintori & Lombardo 1999; Lombardo et al. 2012). Sedimentation took place below wave base and with an often anoxic bottom, as indicated by common laminated limestone or marly-limestone layers and the almost general absence of bioturbation (Tintori 1990; Tintori & Renesto 1990; Tintori & Lombardo 1999, Lombardo et al. 2012). Quite common are also clay-chips beds, often rich also in dark algal-film fragments, probably related to storms affecting the shallower part of the basin or the threshold toward the open waters. The Kalkschieferzone basin was clearly also sometimes affected by sudden fresh water supply following stormy heavy rains, as there is record of several levels rich in conchostracans crustaceans (Tintori 1990; Tintori & Brambilla 1991). In the Kalkschieferzone no sure marine stenohaline organism has been found, apart from the nothosaurid *Lariosaurus* and the fishes, most of them strictly related to the marine environment: in fact, many of the Kalkschieferzone fish genera have been found also in other localities that can be considered surely marine, such as Luoping, in southern China (Lombardo et al., 2011; Lopez-Arbarello et al., 2011) or Perledo along the eastern coast of the Lario Lake (Tintori & Lombardo, 1999; Lombardo et al., 2008) or even the Besano Formation in the same Monte San Giorgio area (Bürgin, 1999).

During the deposition of the uppermost Meride Limestone (the Kalkschieferzone Member), the fresh water influence became stronger and stronger: conchostracans and insects point to a quite close land with superficial fresh-water ponds, permanent or seasonal, as suggested by the number of conchostracan-rich surfaces. Tintori (1990) and Tintori & Brambilla (1991) proposed an alternation of dry and very rainy seasons, a monsoonal-like climate where heavy rains could suddenly hit the Kalkschieferzone basin causing mass mortality events in the marine fauna, mainly fishes, as happened at least for *Prohalecites*, *Peltopleurus* and *Allolepidotus*, but also for the crustacean *Schimperella* (Tintori, 1990).

A further support to the fresh water hypothesis as causing mass mortality in a marine basin after flooding the nearby land, is provided by the assemblage yielding the apterygote insect *Dasyleptus triassicus* (Bechly and Stockar, 2011), from the upper Kalkschieferzone, and by several other surfaces that can be considered as result of a mass mortality event, with at least 20 up to 151 specimens for few square meters (Lombardo et al. 2012).

Furthermore, specimens from a mass mortality surface in the Kalkschieferzone are usually of similar size (Tintori 1990), while less common species, represented by sparse specimens, show a consistent pattern of size grouping (Tintori & Lombardo, 1999; Lombardo, 2002). As already pointed out (Tintori 1990, Tintori & Lombardo, 1999), this also implies that the mortality of marine dwellers was concentrated possibly in a single season of the year even if not always the adverse weather conditions led to mass mortality.

Interbedded to the fish-rich layers, there are levels showing massive quantity of Conchostracans: they are usually almost devoid of fishes (and vice-versa, Tintori, 1990), possibly because when the marine basin was too strongly affected by the fresh waters input from the nearby land for quite a long time, the marine fishes almost totally disappeared from the basin itself.

Apart from the mass mortality surfaces yielding usually *Prohalecites*, more rarely *Peltopleurus* and *Coelatichthys*, all the other fish genera are quite rare and their presence may be related to the attritional mortality in ‘normal’ marine condition.

The Biodiversity of the Kalkschieferzone is quite low: about 20 fish species subdivided in at least two different assemblages (Tintori, 1990; Lombardo, 1999, 2001, 2002; Tintori & Lombardo 1999, 2007; Lombardo & Tintori, 2004), the nothosaurid *Lariosaurus* (Tintori & Renesto, 1990; Renesto et al., 2003), three crustaceans (the mysidiacean *Schimperella*, the conchostracan *Laxitextella* and a very rare undescribed decapod), 19 specimens of insects belonging to eight orders (Krzeminski & Lombardo, 2001; Bechly & Stockar, 2011, Strada et al, 2014) and a few terrestrial plant remains. If the two specimens mentioned by Bechly & Stockar, 2011 are consideres, insects amount to 21 specimens.

The Kalkschieferzone fossil assemblages are not significantly different in the number of vertebrate and invertebrate taxa found in each single level from those from the lower Meride Limestone, such as Cava Inferiore, Cava Superiore and Cassina Beds (Bürgin, 1998, 1999). Instead, the Besano Formation assemblages include many more taxa, both vertebrates and invertebrates (Lombardo, 1999; Röhl et al., 2001) also pointing to a strictly marine environment.

The plant record from the Kalkschieferzone has not yet been described. Tintori (personal communication) remarks that plant fragments form this level are larger and better preserved than in the Cassina Beds, top of the Lower Meride Limestone, as described by Stockar & Kustatscher (2010). Mostly voltziales are present, suggesting a somehow less arid climate than during the deposition of the older levels.

6.1. Taphonomy

The insect collected from site D, Val Mara, are preserved as compression fossils and approximately 30% of the specimens are partially or totally phosphatized.

Phosphatization has preserved both hard (cuticle) and soft parts, showing details of muscles, tendons, internal organs and, in at least two cases, details of the nervous system.

In a few cases, the fossil is preserved on slab and counterslab: anyway, the two slabs never show the ventral and dorsal view of the insects but rather cut through the same view, so that the organic impression is divided between the two slabs.

Fig 8: **A**: Kalkschieferzone succession, Gaggiolo canyon -val Mara - Meride, opposite to the site where the fossil insects were found (Dec 2010): **B**: Clean slates from the excavation

7. *Materials and methods*

All the specimens have been collected in locality D in Val Mara, near Meride (Canton Ticino, Switzerland) and are or will be deposited at Museo Cantonale di Storia Naturale di Lugano. Specimen manipulation and measures were completed with the auxiliary use of the stereo microscope Leica MS5 and an ocular micrometer or with a Parker Hannfin-Deadal Digital Micrometer. Images were acquired by digital camera Canon Eos 450 mounted on a machinery in order to scan the sample at different focus layers that were mounted with Zerene Stacker 1.0 (Student Edition). Drawings were made by camera lucida attached to the microscope or from photographs (when a combination of the characters preserved on slab and counterslab is drawn).

Observationon specimens MCSN8463, MCSN8462 and MCSN8456 were performed on picture series taken with a Zeiss Axioskop 2 was equipped with different objectives of 1.25×, 2.5×, 5×, 10×and 20× magnification under cross-polarized light.

8. Systematic paleontology

In this section the specimens are described and assigned, sometimes tentatively,to a taxon. The degree of preservation of the different specimens is very variable and often the main diagnostic features, as antennae, wings, mouthparts or legs, are lost.

Moreover the type of conservations also plays an important role. In fact, approximaltely 30% of the specimens are completely or partially phosphatized. Phosphatization has allowed the preservation of internal structures normally not visible in fossils, making comparison with other representativesof the same groups very difficult.

Therefore, identification of the specimens, has been possible to the extent allowed by the degree of preservation.

In the following descriptions, phosphatization of single parts is indicated with (P).

At the moment this dissertation was written, the only published specimen, identified as genus and species is MCSN8455, described as *Praedodromeus sangiorgensis* in Strada, Montagna and Tintori, 2014. Other new taxa descriptions will be soon submitted.

8.1. *Specimen* MCSN8451

Systematic paleontology

Order **Coleoptera** Linnaeus, 1758
Suborder Adephaga Schellenberg, 1806
Family Trachypachidae Thomson, 1857
Subfamily Eodromeinae Ponomarenko, 1977
Genus *Praedodromeus* gen. nov.
Type species. *Praedodromeus sangiorgiensis* n.sp. by monotypy.

Etymology. The name derived from the Latin verb "*praedo",* which means to prey, considering its strong and sharp mandibles that we supposed to be used to catch prey, and the suffix "*–dromeus*", which means "runner", from its cursory legs.

Locus typicus: Site D, Val Mara near Meride, Mendrisio, Canton Ticino, Switzerland.

Diagnosis: The general habitus of the new taxon (genus or species), a simple sulcate antenna cleaner in the distal part of the tibiae, the metacoxa separating the thorax and abdomen , the metaepisternum reaching the mesocoxal cavities prompts its ascription to the family Trachypachidae, subfamily Eodromeinae. The new taxon is described as new genus and species due to the presence of a unique set of characters: well developed asymmetrical mandibles; rectangular pronotum, longitudinal groove absent; short metaventrite; and big head with large eyes on the upper surface.

Praedodromeus sangiorgiensis sp. nov.

Holotype: MCSN8451

Etymology. The name derived from the collecting area of Monte San Giorgio (Switzerland/Italy).

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

Description: Almost complete impression in dorsal view, lacking antennae (fig. 9). Head and abdomen in natural position, single disarticulated elytron preserved. Length from apex of mandibules to apex of elytra of 10,8 mm; width at base of elytra of 4,6 mm (length-width ratio 2,34).

All three legs on the right side preserved. Mid and hind femora rather large and robust; maximum width of right mid femora 0,79 mm. Tibiae thin and slender. The preserved tarsi (I+II) elongated and slim; only fore two tarsomers distinguishable, first one enlarged. On the left side preserved only II+III femora and III tibia. Right fore tibiae (length 1,92 mm) harbouring a simple sulcate antenna cleaner organ with enlarged distal area and an apical spur (0,24 mm). Five tarsi (total length 1,62 mm) on I right leg clearly visible. Slender tibiae.

Head big, longer than wider, length of 3,0 mm mandibles excluded and of 3,42 mandibles included, width at the eyes 2,76 mm. Mandibles asymmetrical and triangular, robust and sharp with a small tooth in the anterior second-third of the inner margin. Total length of 1,38 mm, width 0,96 mm, length-width ratio of 1,44. Partial impression of labial palp visible between mandibles.

Pronotum wide (3,1 mm), anterior margin slightly concave with pointed apices (left side), posterior margin straight.

Abdomen partially visible with light impressions of segmentation preserved on the left side. Length of abdomen 1,5 times the length of meso- and metathoraces combined.

Discussion: The specimen has been described based on the preserved morphological characters even if some key characters are lacking, probably due to subaereal degradation before burial. Better-preserved features include the general habitus, the mandibles and the very developed head with dorsal eyes. The new genus differs from *Petrodromeus* (Ponomarenko et Volkov, 2013), *Permunda* (Ponomarenko et Volkov 2013), *Karatoma* (Ponomarenko 1977), *Sinodromeus* (Wang et al. 2012), *Psacodromeus* (Ponomarenko 1977), *Xinbinia* (Hong 1983) and *Fortiseode* (Jia and Ren 2011) for the absence of punctuations ans/or striae on elytra. The genera *Petrodromeus* (Ponomarenko et Volkov 2013), *Permunda* (Ponomarenko et Volkov 2013) and *Karatoma* (Ponomarenko 1977) show a lower head width/length ratio compared to *Praedodromeus* gen. n. The new genus markedly differs from *Fortiseode* and from *Xinbinia* also for the shape of body, pronotum and head. It also differs from *Sogdodromeus* (Ponomarenko, 1977) in the longer abdomen and in the shape of the pronotum. Compared to *Platycoxa* (Ponomarenko, 1977) it differs in the shape of pronotum and mandibles, in the shorter head capsule and smaller eyes. *Praedodromeus* gen. n. differs from *Unda* (Ponomarenko, 1977) and from *Permunda* (Ponomarenko et Volkov, 2013) in the width and shape of the pronotum, which lacks the pointed anterior margins and is less markedly narrower than the base of the elytra. Compared to *Karadromeus* (Ponomarenko, 1977) the new taxon has legs with longer femora, protruding beyond lateral margins of the body and tibiae longer than femora. The comparison with *Beipiaocarabus* (Hong, 1983) is difficult, since the holotype found by Hong is preserved in ventral view, which we are missing. Anyway, apparently in

Beipiaocarabus the abdomen is shorter, the metathorax is quite longer and femora are less strong and thick than in *Praedodromeus*.

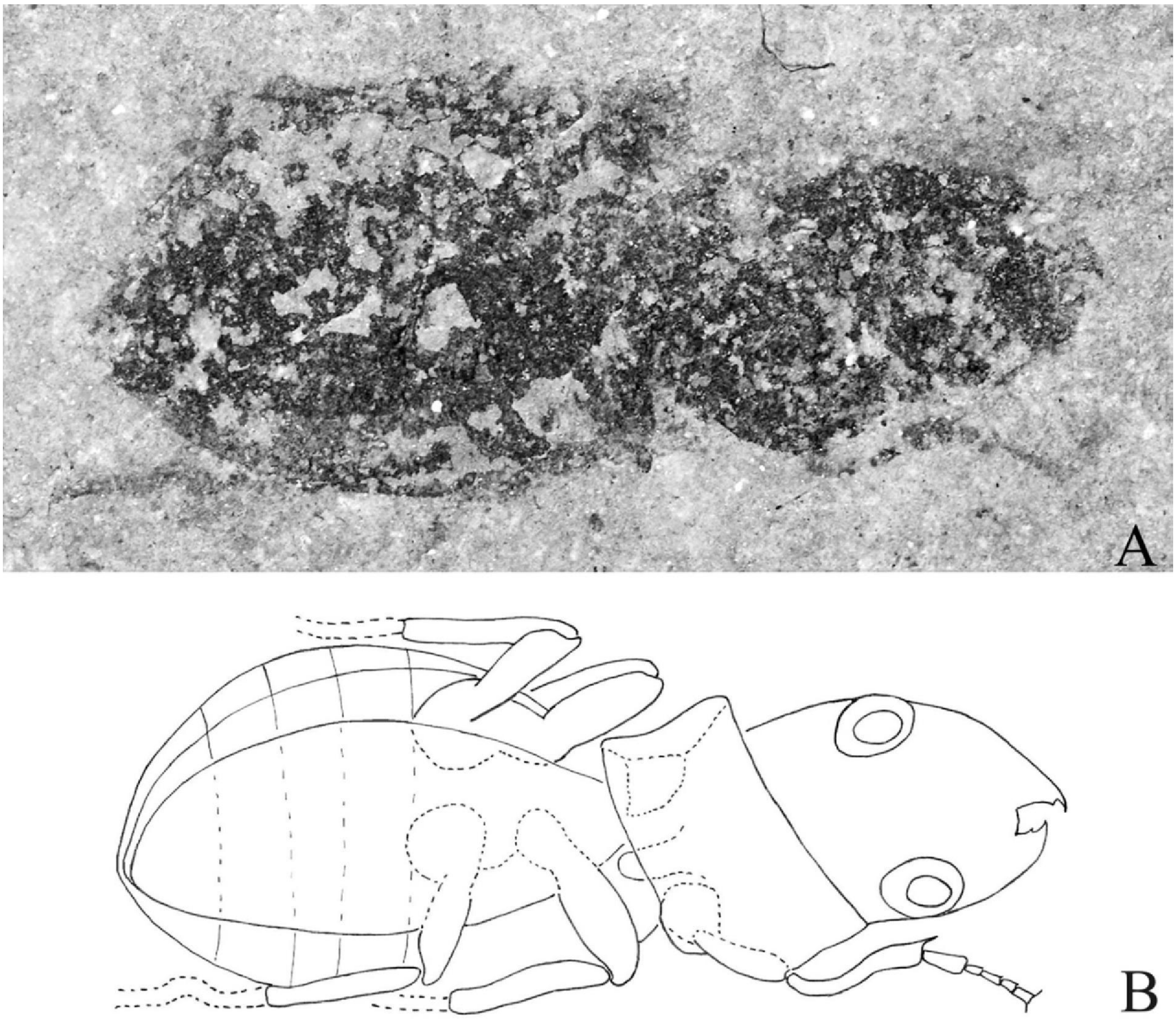

Fig 9 – A:Praedodromeus sangiorgensis gen n, sp n, total length 10.8 mm; B: drawing

8.2. Specimen MCSN8455

Order Coleoptera LINNAEUS 1758

Description: Medium sized beetle, preserved in dorsal view, slab (fig 10 A) and counterslab (fig 10 B). Total lenght 10,31 mm, maximum width at elytra base 4,62 mm. Hydrodynamic, compact body profile. Head short, probably hypognathous, 1,30 mm long and 2,09 mm wide, with a pair of small, dorsal eyes. The eyes show a reddish coloration. Antennae and palpi lost. Elytra 6,69 mm long, 2,31 mm wide. Internal margin almost straight, external margin slightly convex, with steepening angle at approximately 2/3 of the total elytron length. Elytra smooth, with thick epipleural line, clearly visble on the left elytron, preserved in its first third on the counterslab and in the other two thirds on the slab. The epipleura becomes larger towards the end of the elytron. A few traits of the left wing venation are visible on both slabs on the terminal part of the abdomen.

Pronotum 3,03 mm wide, 2,33 mm long. Mesonotum and metanotum not visible, estimated combined length estimated from hind femur position 2,80 mm.

Right legs II and III are poorly preserved and partially overlay, making it very difficult to identify the different leg segments. The hind femur is partially preserved (segment length 0,73 mm) and it’s quite enlarged (maximum width 0,50 mm). The preserved tibia (length 3,19 mm), probably of the third leg, has a tubular and curved shape. A foreleg, femur and tibiae, has detached and is preserved at approximately 1,5 mm from the right side of the head (slab).

No distinctive feature is visible on the abdomen; we can estimate a length of 3,5 mm) and a widthof 3,57 from the hind femur position (as for metanotum).

Discussion: The general habitus of the beetle, its compact and hydrodynamical profile and the thickness of the preserved femur support its assignement to an aquatic group. Unfortunately, no diagnostic features are preserved to allow a definite identification. However, it can be remarked that the beetle closely resembles *Coptoclavella inexpecta* gen. et sp. nov (Soriano, Ponomarenko and Delclòs 2007) from the El Montsec outcrop, Spain, dated Lower Cretaceous (Barremian, 130 – 125 My). *Coptoclavella* belongs to the subfamily Coptoclaviscinae subfam. nov.,one of the five known subfamilies of the family Coptoclavidae (Ponomarenko 1961), an extinct family of aquatic beetles belonging to the suborder Adephaga. Coptoclavids are the most common group of aquatic beetles in the Jurassic and Cretaceous deposits (Wang et al., 2010) and are recovered both as larvae and as adults from the fossil record. They exhibits varying degree of adaptation to aquatic life, but are uniquely characterized by a double pair of eyes for aquatic and subaerial vision. The oldest fossil record of the group so far is a larva described by Ghosh et al (2007) from the Parsora Formation (Lower Triassic if not Permo-Triassic boundary).

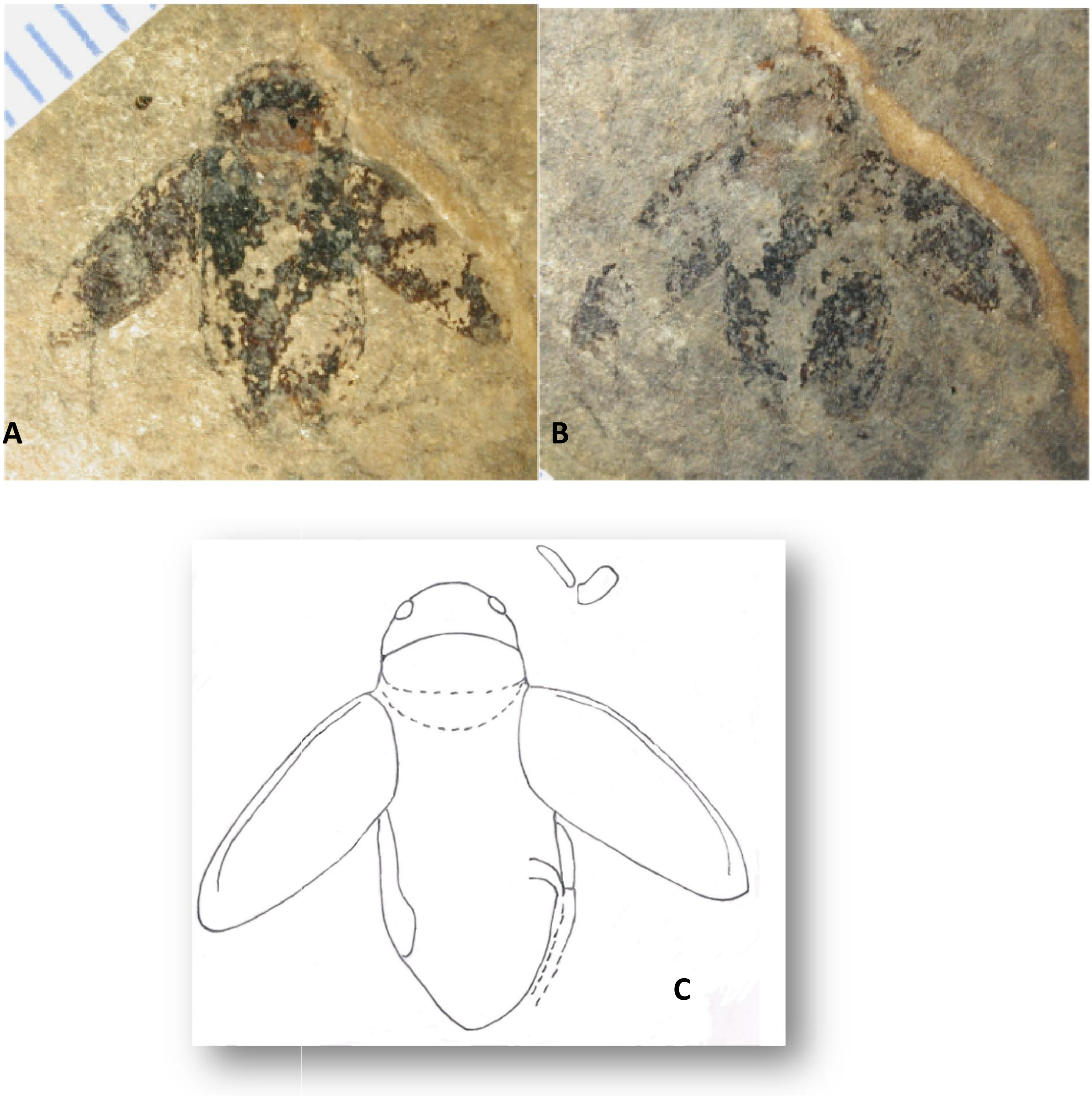

Fig 10: MCSN8455, total lenght 10,31 mm. A: picture, counterslab; B picture, slab; C: drawing combining information both from slab and counterslab.

8.3. Specimen MCSN8461

Order Coleoptera LINNAEUS, 1758

Suborder Archostemata KOLBE, 1806

Description: Fragment of elytron (slab and counterslab), maximum length 2,0 mm, maximum width 0,54 mm (fig 11 A). Circular and sometimes hexagonal cells, tightly packed, wing venation not visible; external rim not visible, possibly not present. Cells are smaller along what might be identified as the external margin of the elytron and in the lowermost and uppermost part of the fragment. Six rows of cells visible in the largest part of the fragment, 18 cells in the longest row. Ornamentation is remarkably similar to that of the whole elytron described by Krzeminsky and Lombardo (2001), that is the oldest known Ommatidae (Notocupes sp) described.

Discussion: In this fragment, no character is preserved to allow us to assign the fragment to the same taxon. Therefore, we can only assign the beetle to the order Archostemata, whose families often exhibit this type of arrangement in elytra ornamentation.

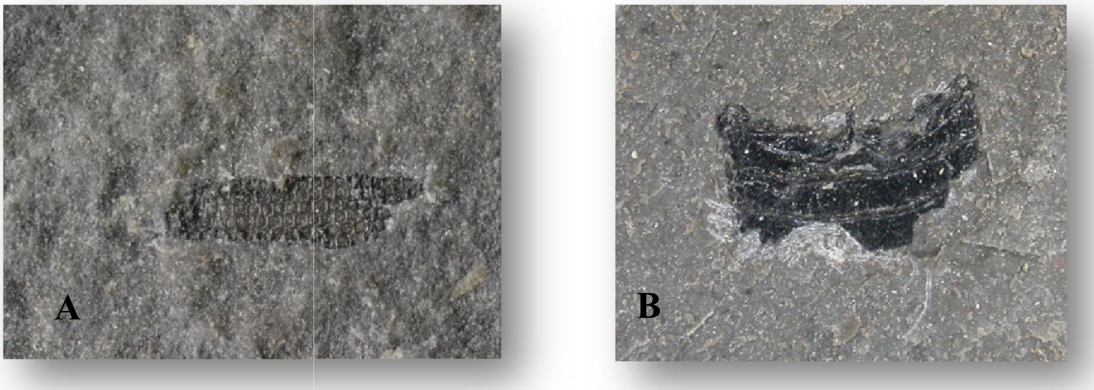

Fig 11: **A**: elytron fragment, slab (MCSN8461), total length 2,0 mm; **B**: abdomen fragment (MCNS8469), maximum width 2,07 mm.

8.4. Specimen MCSN8460

Order Coleoptera LINNAEUS, 1758

Description: Abdomen fragment (fig 11 B), internal side exposed (from comparison with extant Carabid abdomen). Three segments are preserved, no morphological distinctive features and no internal distinctive structures (as leg insertions) are visible. Maximum width 2,07 mm. Length of first segment 0,6 mm; length of second segment 0,52 mm; length of third segment 0,54 mm.

Discussion: since no distinctive features are preserved, it is not possible to classify this specimen beyond the order level.

8.5. Specimen MCSN8464

Order Coleoptera LINNAEUS, 1758

Description: Small beetle (fig. 12), total length 2,90 mm, preserved in dorsal/lateral view, partially preserved. Head appendages missing; legs partially preserved. Pronotum not distinguishable from head; length of head + pronotum 1 mm, width 0,54 mm. Elytra 1,90 mm long and 0,72 mm wide, with faint longitudinal striae. Two femurs, probably from right legs I and II preserved. Femur I 0,41 mm long and 0,17 mm wide. Femur II 0,40 mm long and 0,18 mm wide.

Discussion: The fossil does not preserve any diagnostic feature. The general shape of the body, which is compact and rounded, and of the legs, which show thick femurs, may suggest the assignment to an aquatic group.

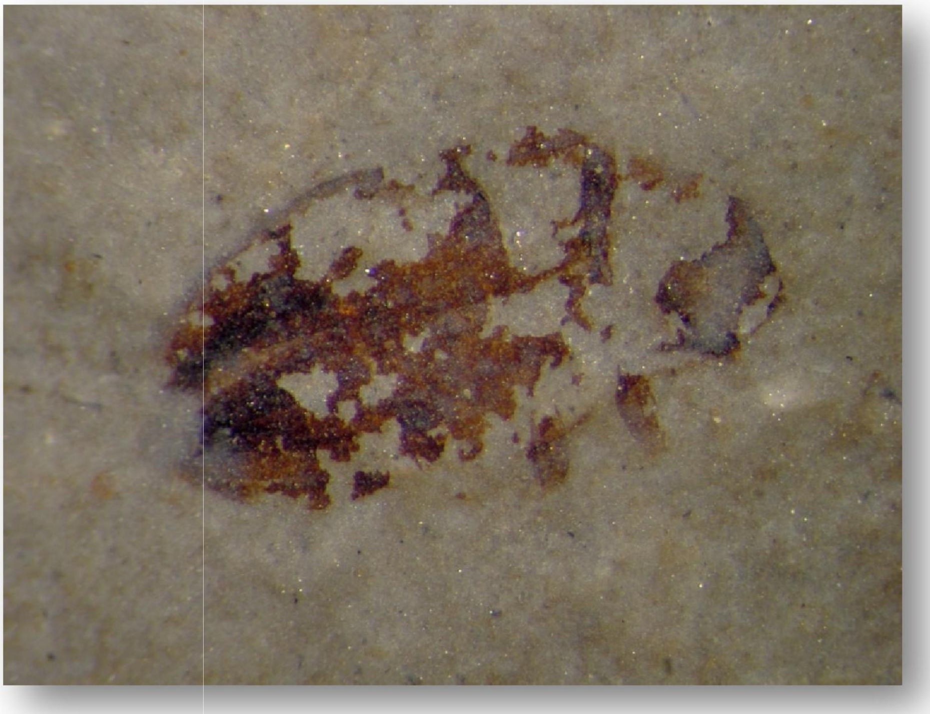

Fig 12: specimen MCSN8464, total length 2,90 mm

8.6. Specimen MCSN8456

Description: Medium sized insect, preserved in a dorsal view, laterally rotated (fig. 13). Total length from top of head to end of wings (terminal part missing): 19 mm. Head capsule preserved, length 3,0 mm, maximum width 1,35 mm, moprhological details not visible. Head hypognathous. Several internal soft tissue structures are preserved (P) under a thin layer of cuticle but are not recognizable; their shape could suggest they are tendons and muscles. No abdominal internal structure is preserved Two appendages preserved (P), probably the maxillary parlps or very thin antennae. Pronotum "T" shaped, embracing laterally the somite in its larger cephalic portion; pronotum maximum width 3,0 mm, length 2,1 mm. Mesonotum preserved, drop shaped, lodged into metanotum, "V" shaped. Mesonotum 2,3 mm long and 1,9 mm wide. Metanotum formed by two segment forming a "V" structure, arms 2,4 mm long and 0,8 mm large. Massive transverse mass (up to 5 mm wide) of compact soft tissue preserved (P) approximately under mesonotum but extending laterally, possibly identified as flight muscles. Left leg I partially preserved (P) in trochanter (0,5 mm), femur (1,0 mm) and tibia (2,05 mm); tarsi missing. Left leg II poorly preserved (P). Left leg III partially preserved, trocanther distinguishable, femur and tibia poorly preserved, distal part missing. The total length of left leg III is 12,0 mm. Very robust right leg III femur preserved (P), 8 mm long and 2,3 mm wide at base. Wings partially preserved, lying at rest on the abdomen, fore wings not distinguishable from hind wings, if both pairs are present. Venation not distinguishable. The terminal part of the wings is missing.

Discussion: At first sight this specimen attracts attention for its apparent good preservation. Unfortunately, a closer examination shows that certain attribution to a group is made very difficult by the loss of important diagnostic features, such as mouthparts, wing venation, eyes/ocelli and tarsi and claws.

The hypognathous head, the shape of the pronotum and, most of all, the thickness, shape and length of femur of the right leg III could support the attribution to Orthoptera. In particular, the distal end of the better preserved femur of right leg III shows a robust articulation recalling those of Orthoptera.

On the other hand, the absence of a fisrt pair of sclerotized wings is not consistent with the orthopteran hypothesys, unless they have been lost. The shape of meso- and metanotum recall those of extant Plecoptera.

Finally, the shape of the head, albeit poorly preserved, shows a resemblance with Isoptera caught in Miocene amber in the pointed terminal part and in the position of the head appendages preserved, that could be interpreted as the thin antennae typical of Isoptera.

At the moment, we cannot carry out a definite assignment of the specimen, but all the orders matched by its characters are from the Polyneoptera superorder. Polyneoptera include Plecoptera, Zoraptera and Embiodea; Orthoptera and Phasmatodea; Dermaptera; Grilloblattodea; Mantophasmatodea; Blattodea, Isoptera and Mantodea and most of these orders were already well developed in the Triassic.

Fig 13: specimen MCSN8456, total length 19 mm

8.7. Specimen MCSN 8457

Description: Poorly preserved insect (fig. 11), entirely phosphatized with the exception of a dark unresolved bulk probably in the meso- and metathorax position. It is not possible to determine whether the ventral or the dorsal sight is preserved. Femora (I, II, III), left and right, are preserved. An irregular structure is visible on the first half of the external margin of left femur III.

Length of preserved leg segments: femur I, right: 2,58 mm; femur I, left: 2,49 mm; femur II, left: 2,89 mm; femur II, right: 1,98 mm; femur III, left: 5,93 mm; femur III, right 6,53 mm.

A bundle of tubular structures is preserved in the abdomen, forming an important mass. Due to their position, they are here interpreted as Malpighian tubes, that have origin from the pylorus at the midgut-hindgut border. It must be noted that they show an alternation of white and dark segments, that might suggest the alternation of full and empty traits. This is unsusual for the extretory system therefore a very convolute proctodeum cannot be excluded.

An unidentifiable symmetric structure is also preserved in the terminal part of the abdomen.

Discussion: The specimen has been tentatively assigned to Orthoptera for the length of its hind femora and their position, parallel to the body longitudinal axis, which is typical of orthopteran legs at rest.

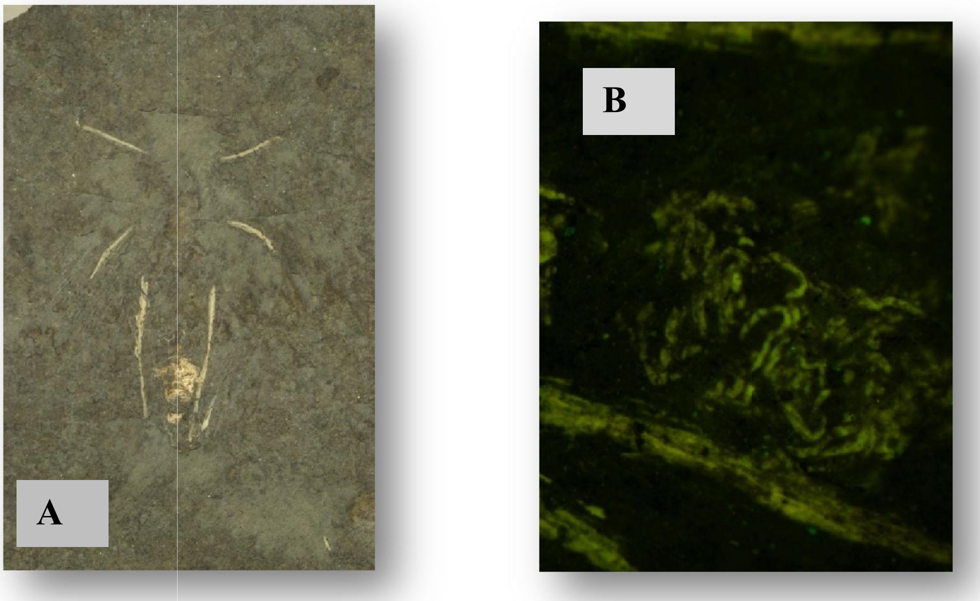

Fig 11: MCSN 8457 **A**: pitcure of the whole specimen in normal light; **B**: detail of the Malpighian tubes, objective 10 X, blue light.

8.8. Specimen MCSN8457

Order Embiodea KUSNEZOV, 1903

Diagnosis: both fore basitarsi swollen (right fore basitarstus 0,61 mm long, 0,51 mm wide; left fore basitarsus 0, 53 mm long, 0,43 mm wide). Three segmented tarsus, two more segments being preserved after right basitarsus. Long fore legs, shorter and thinner middle legs, stronger hindlegs with enlarged femora (right and hind femora 0,73 mm wide).

Desription: medium sized insect preserved in ventral view (Fig. 16), total length 18,28 mm. Head and all legs partially preserved, phosphatized. Thorax and abdomen poorly preserved, not phosphatized, and maintaining some of their original dark brown coloration. Head rather big, longer than wider, as can be inferred from the insertion of antennae (partially preserved) and maxillary palp, 1,43 mm long, visible on the left side of the head. The last segment of the right maxillary palp is preserved and a segment of the right antenna is visible. Mandibles not visible. No structures are distinguishable from the posterior part of the head. All legs are preserved phosphatized (fig 12 A, B, C, D) and the internal soft tissue structures, muscles and tendons, are visible. Both forebasitarsi preserved, enlarged, slightly drop-shaped. In the right fore basitarsus the muscle structure of the following segments is preserved. Right tarsus composed of three segments, total length 1,49 mm. Leg I total length, estimated from left leg I femur and tibia plus right leg I tarsus: 5,02 mm. Left leg II preserved; femur 1,22 mm long, 0,57 mm wide; tibia 0,95 mm long; tarsus 0,56 mm long. Right leg II preserved; femur 1,42 mm, tibia 1,33 mm, tarsus 0,55 mm. Left leg III preserved femur 2,25 mm long, 0,73 mm wide; tibia 2,25 mm long; tarsus 1,22 mm long. Right leg III preserved femur 1,95 mm long, 0,73 mm wide; tibia 1,99 mm long; tarsus 0,69 mm long. Tibiae of legs II and III enlarged at the end. What could be pro-, meso- and metatergites partially preserved, retaining a dark brown coloration. Separation between the three thoracic somites poorly preserved; length of pro- + meso- + methathorax 7,29 mm, estimated from the distance between the point of insertion of left leg I and III. Abdomen not preserved, except for the distal part of the last segment (genitalia?) preserved phosphatized, poorly resolved. Abdomen length, estimated from the insertion point of femur of leg III and the apex of the last segment: 5,69 mm. Two structures are visible at both sizes of the thorax, each formed by two thick lines of grey matter, 3 mm long and 0,2 mm thick, disposed in an approximately triangular shape with the apex pointing to the tail of the insect.

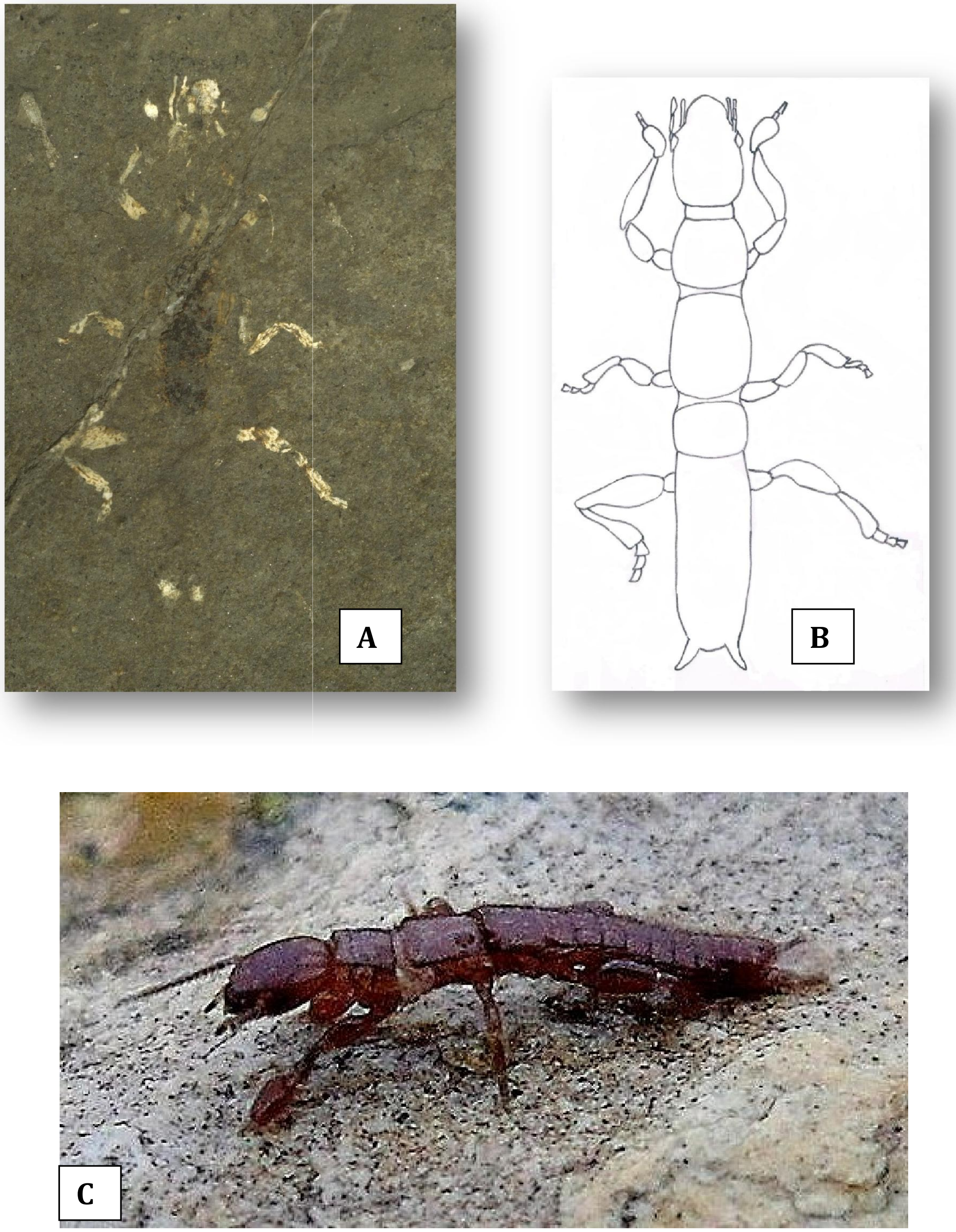

Fig 15: specimen MCSN8457 **A**: picture, total length 18,28 mm; **B**: reconstruction of a possible the body profile; **C**: extant *Haploembia solieri* (fam Oligotomidae), from the web (http://villenatura.blogspot.it/2012/07/haploembia-solieri.html)

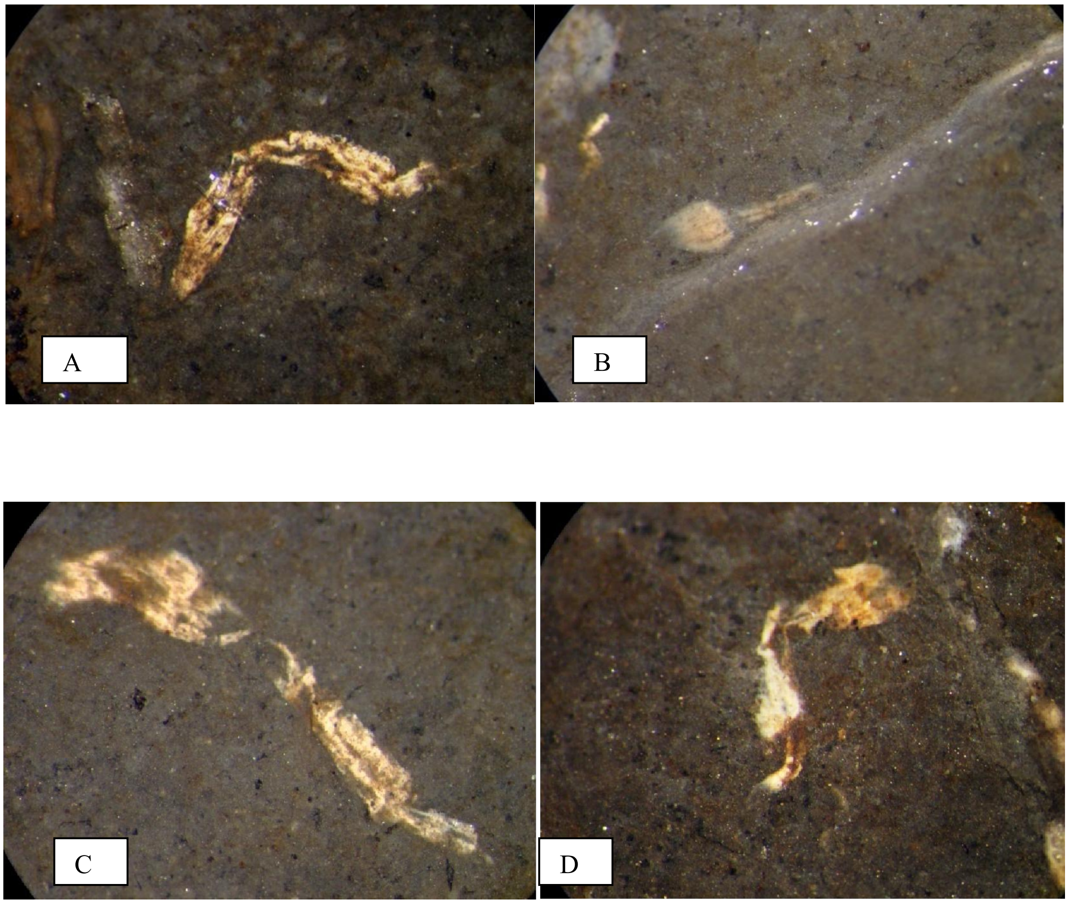

Fig 16: MCSN8457, magnification at 4X. **A** right leg II; **B** right forebasitarsus; **C** right leg III; **D** left leg II

Discussion: at the moment, 11 species of fossil Embiodea are known (Cockerel, 1894; Davies 1939; Engels et al, 2011, Engels et al, 2011; Huang and Nel, 2009; Ross, 1956, 1984; Szumik, 1994; Szumik, 1998). They are from the Cretaceous (two species), from the Eocene (three species) and from the Miocene (four species). These species have all be assigned to the suborder Neoembiodea (Engel and Grimaldi 2006). Two more species, *Sinembia rossi* and *Juraembia ningchengensis* gen. et sp. nov., have been described by Huang and Nel (2009) from the Middle Jurassic of Inner Mongolia, China. MCSN8457 shows the most important character defining Embiodea. In fig 15 B a possible reconstruction of the insect is proposed. Most of the dimensions reported in the description were taken on phosphatized parts. Since they are internal organs, in most cases muscles, it is probable that size is underestimated.

On the other hand, it is not possible to compare it with the other fossil species, due to the loss of other relevant features such as mandibles, genitalia, setae. For this reason we have decided not to erect a new taxon, despite the long time interval between this fossil and the nearest fossils Embiodea from the Jurassic. But we still feel this specimen is an important finding since it extend the range of Embiodea fossil record of approximately 25 My years.

MCSN8457 shows the perfectly developed order synapomorphy represented by the enlarged fore basitarsi. The two symmetrical grayish structures on both sides of the thorax cannot be surely identified. However, their position and symmetry could suggest they are the remains of the enlarged wing veins through which Embiodea can pump hemolymph to collapse or extend their wings to facilitate motion through their silk galleries. On the other hand, MCSN8457 apparently shows two peculiar characteristics: a thick body and tarsi on legs II and III markedly enlarged at their distal extremity. The body outline can be inferred from the distance between the two femurs of the same pair of legs: it is not impossible that partial preservation of the somites of both thorax and abdomen and the loss of all trocanthers can overestimate body diameter. Concerning the tibiae, only the muscles are preserved and the outer form of the leg could be different and more similar to the other representatives of Embiodea.

Engel and Grimaldi (2006) suggest a Triassic origin for Embiodea: MCSN8457 seems at least to confirm this hypothesis but, given the perfectly affirmed salient character of the order, the silk spinning organs, it could suggest an even more ancient origin.

8.9. Specimen MCSN8462

? Order Plecoptera LATREILLE, 1802

Description: completely phosphatized specimen, preserverd in dorsal view. Total length 9,38 mm. Head and thorax well preserved; abdomen partly preserved. Only a very partial impression of three legs.

Head prognathous, mandibles preserved, smooth and symmetrical, no teeth present. Head length 1,13 mm. Maxillary palps preserved, possibly, three segmentes, 0,90 mm long. The muscles extending from the insertion of the palps into the head are visible. Head anterior to head appendages insertion point 0,79 mm long, 0,65 mm wid . Head width at the eyes (beyond insertion of the preserved head appendages) 1,61 mm.

Pronotum 0,94 mm long, 1,34 mm wide. Two pairs of wing stubs are preserved. First pair maximum length 1,21 mm, second pair maximum length 1,14 mm. Mesonotum length 0,94 mm, metanotum length 0,98 mm.

Abdomen length 4,36 mm, maximum width 2,02 mm, Apparently, the distal part is damaged and partly missing. The denser white mass visible in the second half of the abdomen shows the structure of the Malpighian tubes. The remaining internal structures are not distinguishable.

Three legs are poorly preserved, probably the femurs of left leg II and III (length 1,30 mm) and of right leg I (length 1,42 mm). Femurs thick (thickness right femur I 0,314 mm, left femur III 0,416 mm).

In the head, part of the nervous systems is preserved (fig. 15). The protocerebrum is well defined (the deutocerebrum is not visible, being beyond the protocerebrum) and the tritocerebrum is visible. The structure is 0,275 mm wide in its central part, 0,588 mm wide including the two lateral lobes and 0,368 mm long until the emergence or the circumesophagean connettives. The right lobe is almost completely preserved and it's 0, 249 mm long and 0,241 mm wide. The outer portion of the left lobe is missing. From the center of the protocerebrum, a nervous tracts depart, probably towards the two lateral ocelli. The two lobes of the protocerebrum on each side project towards a roughly triangular structure that could be formed by the optic nerve and the optic lobe. From the center of the protocerebrum the double nerve cord projects backwards and after 0,518 mm forms the subesophageal ganglion, very poorly preserved only in its most proximal part (0,126 mm long).

Discussion: the fossil is of difficult interpretation, due to the conservation of almost exclusively internal structures. The presence of two pairs of wing stubs is the sure indication of a hemimetabolic taxon. A tentative receontruction of the appearance of the insect is provided in fig 17 B, but of course it leaves a lot to personal interpretation. My opinion, not supported by experts of the order, is that it is a Plecopteran larval stage.

However, the preservation of the nervous structures and of the Malighian tubes is so exceptional that makes this fossil extremely significant despite the only tentative identification.

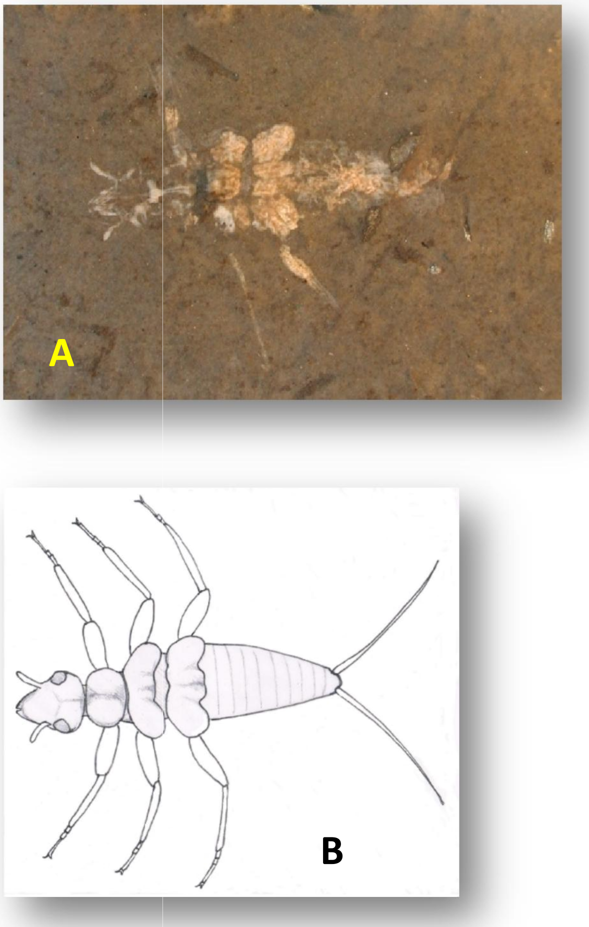

Fig. 17:A:specimen MCSN 8462, total length 9,38 mm; **B** reconstruction of a possible body profile. specimen

8.10. *Specimen* MCSN8459

Order: Hemiptera LINNAEUS, 1758
Suborder: Heteroptera LATREILLE, 1810
Family: Tingidae LAPORTE, 1832

Diagnosis: ornamented wings, with areole; pronotal disc, ornamented, extending over the head; trimerous tarsi; mouthparts forming a piercing/sucking rostrum; head elongated.

Description: specimen preserved in ventral view, slab and counterslab. Total length 11,81 mm. head, thorax, abdomen, five legs preserved. Head appendages and wings II lost. Fragments of hemelytra visible superimposed on thorax and abdomen.

Head poorly preserved, 1,52 mm long, 1,43 mm wide. No morphological details visible apart from two segments of the rostrum (circle on fig 16 A and B) resting on the mesonotum and reaching at least the end of mesothorax. Impression of the eyes visible on counterslab; eyes of medium size, globular, projecting laterally outside the head . Neck width 0.80mm. Antennae lost.

Outile of the pronotal disc visible on the counterslab, 2,55 mm large at the base of the neck. Thorax 4,67 mm long, 4,53 mm wide. Form the ventral view, the pronotal disc seems to cover and embrace the entire length of the head.

Abdomen length 6,13 mm, approximate width at base 4,498 mm. Genital capsule partially reserved.

External margin of hemelytra with areole visible on the left side of the abdomen on slab, right side on counterslab, and on the right of the thorax on counterslab. Areole rather large, areola on tip of hemelytra at the left side of the abdomen 0,643 mm wide. Hemelytra protruding from abdomen for approximately 0,5 mm.

Five legs preserved: right leg I, dislocated on the left side, over left leg I; right leg II; left leg I, II and III. right leg II femur 2,16 mm long; tibia 2,41 mm long. Left leg I 1,65 mm long. Left leg II femur 2,15 mm long; tibia 2,25 mm long. Tarsi partially preserved from left leg II, 1,067 mm long. Tibiae of the forelimbs enlarged, 0,625 mm thick (left leg).

Discussion: Present knowledge about the evolution of Tingidae is hampered by the scarcity of well-preserved Mesozoic fossils. The group known fossil record spans from the Lower Cretaceous to the Miocene (Wappler, 2003) but the origin of the family is placed in the Cretaceous. MCSN8459 brings back the origin of Tingidae even further, into the Triassic. The state of preservation prevents comparison with finer structures, as parts of the head and head appendages, but the main characters of the group are already represented. The largest differences with more recent fossil Tingidae and with modern ones lie in the enlarged and shortened tibiae of the first pair of legs, in the long, trimerous, hook shaped tarsi and in the specimen size, wich is over the range of extinct and extant species (two to eight mm, with most species falling within a maximum size of five mm). The shape and dimensions of the areole are interestingly similar to those of extant genera, compared to the those of other and more recent fossil lace bugs, which show thickest sclerotization and smaller cells.

Today lace bugs comprise over 2100 species belonging to approximately 300 genera and are present in all major zoogeographic regions (Drake and Ruhoff, 1960; Froeschner, 1996). They are exclusively phytophagous, the most common species occurring on the foliage of trees and shrubs.

Fig 18 – MCNS8459, **A**: counterslab; **B**: slab. Total length 11,81 mm; **C**: MCNS8459 drawing; **D**: an extant Tingidae: Acalypta parvula from the web (http://www.britishbugs.org.uk/heteroptera/Tingidae/acalypta_parvula.html)

8.11. Specimen MCSN8463 and MCSN8466

Order Archaeognatha Börner, 1904

Family Machilidae Grassi 1888

Diagnosis. Paired segmented cerci at the abdominal apex and of the basal part of the terminal filament, large segmented maxillary palps and abdominal styli prompts the ascription of this insect fossil in the apterygote order of Archaeognatha (=Microcoryphia). The presence of the styli-like appendage on the metacoxae, appendages covered with scales (clearly visible on the third leg pair, partially on the second) and the presence of eversible vesicles on abdominal coxites I-V are diagnostic featres of Machilidae.

Description. Huge machilids, total body length of 39.5 mm (holotype), which is double than the largest Machilidae so far known, both extinct and extant. Both specimens in ventral-dorsal view with exoskeleton and soft tissues preserved. The description is based on MCSN8463 (fig. 19) since MCSN8466 (fig 20) is only partially preserved (abdomen and metathorax; the size and the preserved anatomical features of MCSN8466 confirm the ascription to the same taxon as MCSN8463.

Specimen with head and thorax slightly rotated in the sagittal plane. Body length of 39.5 mm (from the apex of the cephalic region to the last abdominal tergite) and width of 8,94 mm (second thoracic somite) (Fig. 19). On the cephalic region three pairs of appendages are preserved: *i*) the proximal part of antennae (scapus and pedicellus) and a portion of the multi-segmented flagella (length 2.28 mm); *ii*) the first three segments of the large leg-like maxillary palps (length 2,284 mm); and *iii*) prementum (3,538 mm in length, 1,180 mm in width). The terminal segment of the right labial palp is preserved. In the thoracic region coxae, trochanters and femurs of fore, mid and hind legs (the latter on the left side only partially visible) are preserved. On the surface of the hind trochanter, setae (348 µm long) and scales are visible. A styli-like appendage (1,888 mm in length) is present on the metacoxae (Figs. 21 c, d). On the right side of thorax pro- meso- and metanotum are visible from below. Mesonotum is partially visible also on the left side. The abdomen is composed by 11 visible urosternites (urosternite I only partially visible on the left side), the last urosternites harbor the proximal part of the two cerci. Coxopodites and sternites from I to VIII are clearly visible, coxopodal vescicles present on coxopodites from I to VII, the second coxopodal vescicle is visible on ventral abdominal plates II (both sides) and IV-V (right side) (Fig. 22 a - d). Abdominal styli are clearly visible on abdominal plates II left and IV right.

Noticeably, in MCSN8463 soft tissues are preserved, namely parts of the central nervous system and muscular bundles within legs and abdominal plates. The following structures of the central nervous system, are preserved: *i*) the two optical ganglia and a portion of the proto- deutocerebrum in the cephalic region, and *ii*) a partial ventral nerve cord composed of three pairs of abdominal ganglia with their connectives (Fig 19). Abdominal (*a*) ganglion 6*a* length 550 µm, width 368 µm; ganglion 7*a* length 570 µm, width 340 µm, ganglion 9a length 337 µm, width 225 µm. On the external boundary of the optical ganglia the typical compound eyes structures are present. From the outside to the inside the corneal surface (*cs*), the lens layer (*ll*) and crystalline cone (*cc*) can be identified. Right eye: major axis 2.25 mm, total thickness of *cs* + *ll* 222 µm. These structures are clearly visible on the right optical ganglion while they are partially visible on the left. In both optical ganglia, below the three layers structure, the lamina, the outer and inner chiasma, the neuropils medulla (*me*) and the lobula (*lo*) are preserved. Muscular bundles, hypothesized as femur-trochanter and adductors muscles are preserved respectively in the left mesotrochanter and within the right hind leg in coxa and trochanter (Figs. 21 a, b). In addition, within abdominal plates from I to IV retractor and stylet muscles are visible

Fig 19 specimen MCSN 8463 total length 39,5 mm

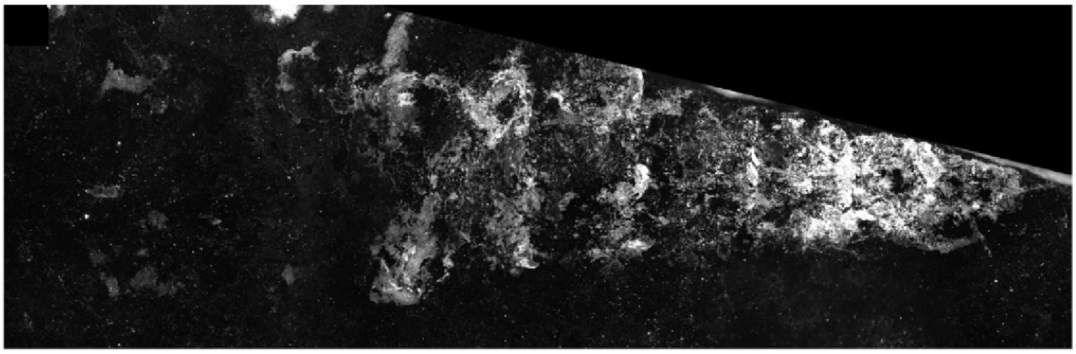

Fig. 20. MCSN8466.

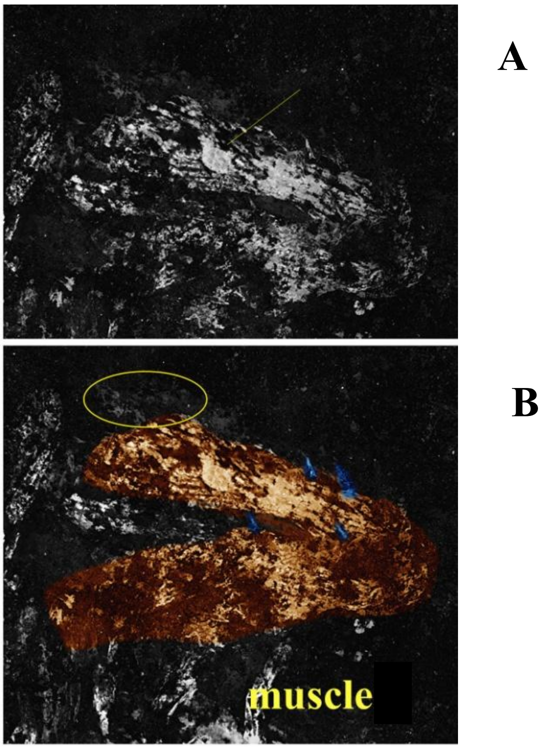

Fig 21: Details of MCSN8463. A. Close-up on thoracopod. **B**. Colour-marked version of **A**

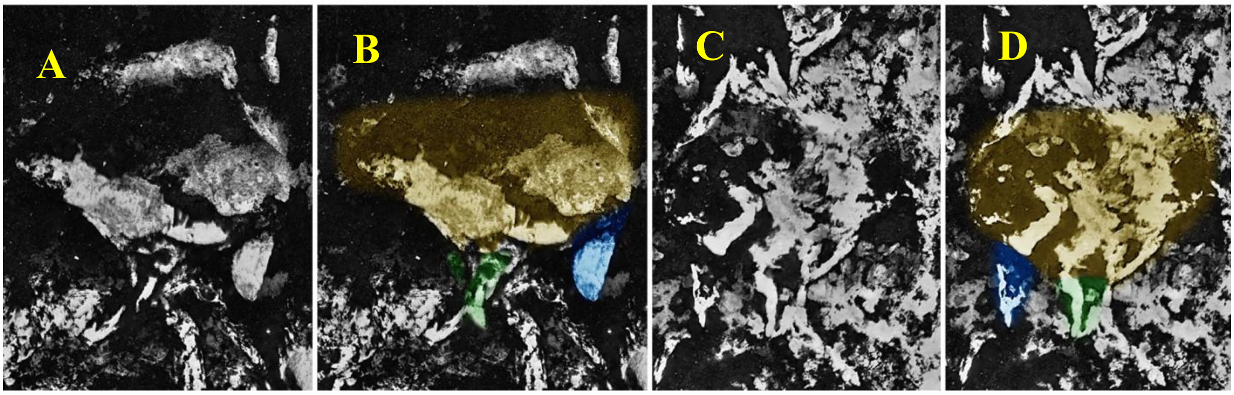

Fig. 23: *Dasyleptus brongnarty* Sharov form the late permian of Kaltan, South-Western Siberia. Form Rasnitsyn and Quicke, 2002.

Discussion. The exceptional preservation of soft tissues MCSN8463 has been possible through the process of phosphatization, an extremely rare event that has been reported in very few cases, namely Chengjang (Cong et al, 2014; Ma et al. 2012; Tanaka et al, 2013) and one case among the fossils of the Burgess Shale (Strausfeld, 2011). The central nervous system preserved in this specimen exhibits a homonymous metameric pattern, confirming the hypotheses on the evolution of this structure. The idealized concept that the insect's ancestor possesses a segmental pervasivity with a perfectly segmented ventral nerve chord, hypothesized on the basis of extant taxa, has been here firstly demonstrated in a ~240 Mo fossil by the presence of the segmented four pairs of abdominal ganglia with their connectives matching the abdominal segmentation. Noteworthy, the structures of the optical ganglia highly resemble those possessed by extant insects.

The specimen is a member of the family Machilidae, and therefore contributes to shed light in the Archaeognatha evolution. The fossil record of Archaeognatha (bristletails plus †Monura) is sparse and is often represented by fragmentary material. It spreads from Late Devonian (Labandeira et al., 1988) to Miocene (Sturm and Poinar, 1997). So far, the majority of findings belong to the genera *Dasyleptus* (†Monura; †Dasileptidae) and *Machilis* (Machilidae). The oldest fossils, represented by fragments, date back to

Devonian period: a head capsule plus a thoracic fragment from Gaspé Bay (390-392 My; Labandeira et al. 1988), and a partial terga plus an eye fragment "tentatively identified as belonging to machilid insect" from Gilboa (376-379 My; Shear et al., 1984). Complete or almost complete specimens have been described only for the extinct Monura, represented only by the genus *Dasyleptus* (fig.23). Interestingly, a member of †Monura, *Dasyleptus triassicus* (Bechly & Stockar, 2011), has been described from the same stratigraphic unit of MCSN8462, extending the presence of *Dasyleptus* well after the end-Permian mass extinction. Fossil of sure attribution to Machilidae are from the Eocene (Koch and Berendt, 1854; Menge, 1854; Olfers, 1907; Silvestri, 1912; see for a review Getty et al. 2013; Mendes & Wunderlich 2013). The only other fossil from Upper Triassic, *Triassomachilis uralensis* (Sharov 1948) has been recently confirmed as a mayfly larva (Sinitshenkova, 2000). Therefore MCSN8462 traces back the origin of Machilidae in the Middle Triassic, extending the range of the extant family of about 200 Ma. This finding is in agreement with those obtained in a recent study on insect phylogeny based on genomic data, in which the last common ancestor of extant Machilidae and Meinertellidae has been dated to 145.6 My (CI ~325-33.3 Ma; Misof et al., 2014).

9. General discussion

The specimens have already been discussed individually. Therefore, here the focus will be on the insect assemblage as a whole, on its paleoenvironmental significance and on some exceptional features of this entomofauna. Also the taxa described by Krzeminski and Lombardo (2001) and by Bechly andStockar (2011) will be included in the discussion on the assemblage.

As a general remark I must stress that systematic paleontology was strongly influenced by the state of preservation of the specimens, which was very variable, and by the type on conservation.

9.1. The Kalkschiefezoner insect assemblage and its paleoenvironmental implications

9.2. The insect assemblage

The fossil assemblage from the Kalkschieferzone of Monte San Giorgio is very diverse. Even if the identification of two of the 16 specimens studied is only tentative, it includes representatives of seven orders. Table 2 shows the list of the identified taxa from val Mara site D, the number of specimens for each taxon and their living environment, based on the assumption that the living environment of fossil groups can be inferred from that of extant relatives. *Tintorina meridensis* and *Notocupes* sp from the work of Krzeminski and Lombardo (2001) are included.

Among the insects of Monte San Giorgio, four specimens are to be considered exceptional findings regarding the Paleontological Record.

The specimen of *Notocupes* from MSG is the oldest record of the genus, as *Praedodromeus sangiorgensis* (Strada et al, 2014) is the oldest fossil Trachipachydae.

Specimen MCSN8463 is by far the oldest complete Archaeognatha so far recovered,supported also by MCSN8466. the next more ancient specimen being *Cretaceomachilis libanensis* (Sturm and Poinar, 1998) from the Lower Cretaceous (thus more than 130 My later) of Lebanon and assigned to the family Meinertellidae. Besides, they have exceptional size, suggesting an unsuspetcted early radiation for the group.

Order	**Family**	**Species**	**N° of specimens**	**Living environment**	**Posphatization**
Ephemeroptera	Tintorinidae	*Tintorina meridensis*	3(adults)	Strictly freshwater for reproduction and life through all the immature stages; in clean still or running waters. Larvae feed on plant or, more rarely, animal debris	Absent
Archaeognatha	Machilidae (s.str)	nd*	2	Damp environments, under bark of trees, in soil or leaf litter or in rock crevices. Some inhabit rocks at the base of coastal cliffs, others favour rainforest environments	Complete
?Orthoptera	nd*	nd*	2	Preferentially terrestrial habitats although some species live on the shores of ponds, streams, lakes, and rivers phytophagous, otherwise carnivorous/predatory	Partial/Complete
?Plecoptera	nd*	nd*	1(nymph)	Freshwater, clean, cold and running waters. Phytophagous or predatorial habits	Complete
Embioptera	nd*	nd*	1	Strictly terrestrial and phytophagous. Silk producing organs in modified tarsi	Almost Complete
Hemiptera	Tingidae	Gen. and sp. nov.	1	Terrestrial, phytophagous	Absent
Coleoptera	Trachypachidae	*Praedodromeus sangiorgiensis*	1	Strictly terrestrial habitat, both in the larval and adult stage, with predatory habits, extant species (Tracypahinae) dwell in loose soils	Absent
Coleoptera	Ommatidae	*Notocupes*sp.	1	Strictly terrestrial. Larvae: wood borers, feeding on dead, fungi infested wood. Adults live in dead subterranean wood such	Absent
Coleoptera	Cupedidae ?	nd*	1 (elytron, fragment)	Strictly terrestrial. Larvae: wood borers, feeding on dead, fungi infested wood. Adults live in dead subterranean wood such	Absent
Coleoptera	Coptoclavidae?	nd*	1 (adult)	Freshwater. Predatory habits	Absent
Coleoptera	nd*	nd*	1 (abdomen fragment)	nd*	Absent
Coleoptera	nd*	nd*	1 (adult)	Possibly aquatic	Absent

Tab 2: identified taxa, number of specimens and living environment for each taxon, based on the assumption that the living environment of fossil groups can be inferred from that of extant relatives; type of preservation.

It is noteworthy that in the same stratigraphic unit at Monte San Giorgio coexist specimens of Archaeognatha with different bauplan: *i*) the ancestral represented by the monuran *D. triassicus*; and *ii*) the new represented by MCSN8462. The former, according to the fossil record, was near to its extinction while the latter was possibly at the beginning of its radiation. It has been observed that *Dasyleptus* markedly resembles the larval stages of extant species (Rasnitsyn 1980, 2000). Therefore, two hypothesis could be formulated in order to provide possible explanations concerning the co-occurrence of these two forms: *i*) all members of the extinct †Monura, including *D. triassicus*, recovered from Upper Carboniferous to Middle Triassic are larval stages of unknown adult forms, possibly resambling extant Archaeognatha; or, *ii*) fossils described as *Dasyleptus* spp. (†Monura) are both adults and instars of separate taxa. Even if the first hypothesis is still debated (Grimaldi, 2001, 2010; Rasnitsyn 1980, 2000), Rinehart et al. (2005), demonstrating the presence of six instars in the record of *D. brongniarti* from Kuznetsk Formation (Middle Permian), estimates an adult size between 15 and 20 mm (see fig. 24 for comparison of MCSN8462 with *Dasyleptus* morphology and size). We thus consider the first explanation highly improbable and we hypothesize that the new plan arises from the ancestral, represented by *Dasyleptus*, making a step forward in the evolution of the taxon as shown in figure 25A. In figure 25B is reported the commonly accepted pattern of Archeognatha evolution before the finding of this specimen. In fig 26 a modern Machilidae s.str.

Specimen MCSN8459, assigned to Tingidae (Hemiptera: Heteroptera) is the most ancient fossil record of the family by 130 My, the oldest fossil record so far being from the Lower Cretaceous. It has unsusual characters, namely the enlarged tibiae, trimerous hooked tarsi and exceptional dimensions, being twice the average size of the group, and four mm longer than the maximum length range of the family (8 mm), taking into account both extinct and extant species.

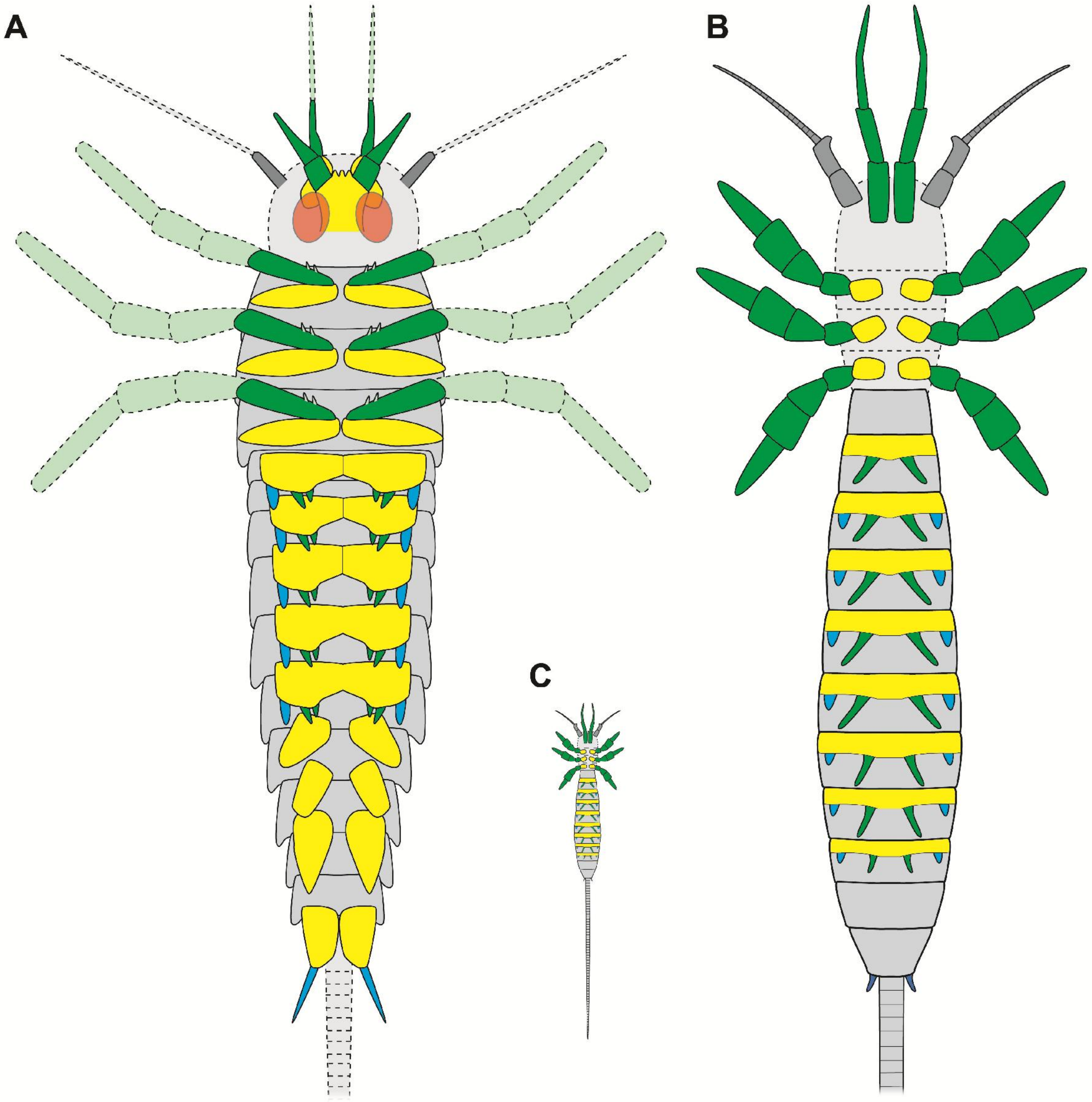

Fig. 24. Schematic reconstruction of MCSN8462 and *Dasyleptus triassicus* in ventral view. Colour scheme following Walossek (1993): coxa or coxopodite (= basipod of Euarthropoda) in yellow; endopod and derivatives in green; exopod derivatives in blue. A. MCSN8462B. *Dasyleptus triassicus*, based on Bechly and Stockar (2011); note that two pairs of ventral structures have been reconstructed: a further median one originally interpreted as the styli is here re-interpreted as eversible vesicles (due to position correlation; in green), and further lateral smaller ones as styli (in blue). C. Same as B. but in the same scale as A to show size ratio of the *Dasyleptus triassicus* and MCSN8462. Drawing provided by Dr. Joachim Haug, from the University of Munich (LMU), Department of Biology II

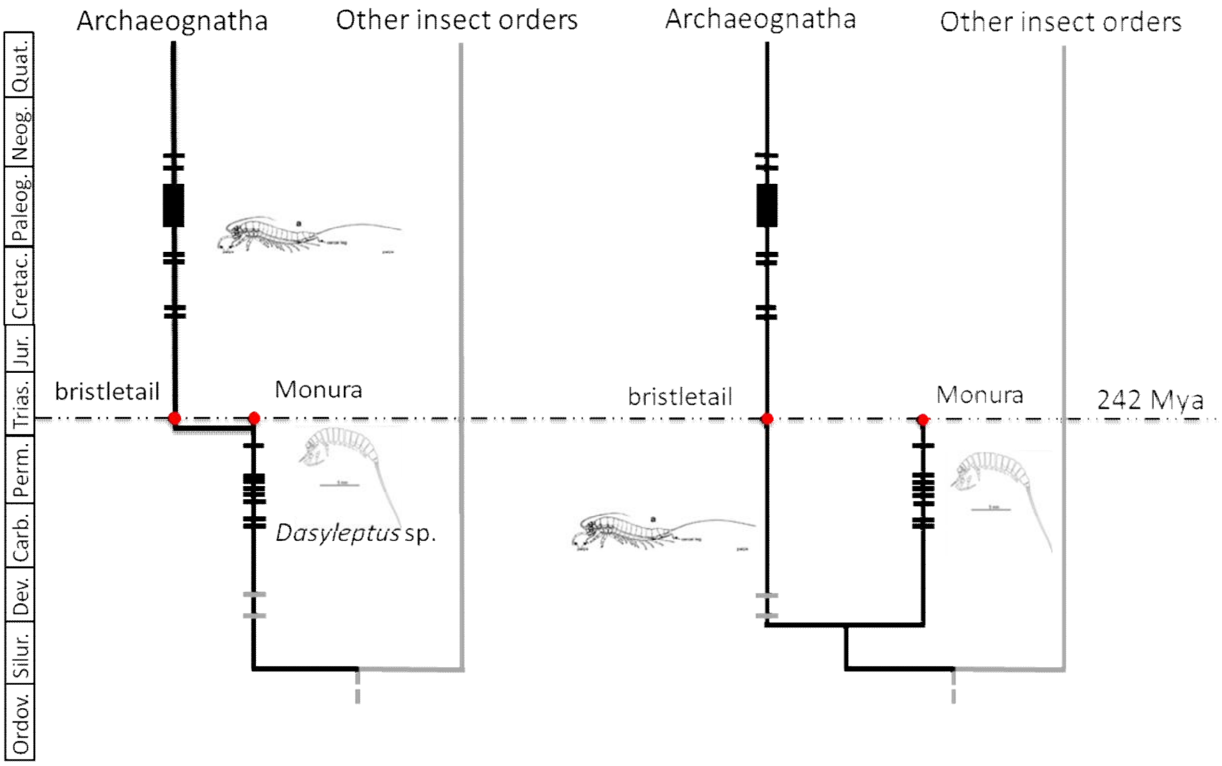

Fig 25 A: Alternative scenarios proposed for Archaeognatha (Machilidae s.l. and †Monura) evolution. **A**. Evolution of extant Archaeognatha in the Permian-Triassic period from a monuran-like ancestor. **B**. Evolution of extant Archaeognatha in the Silurian period

Fig 26: an extant Machilidae s. str., *Trigoniophthalmus alternatus* (http://www.naturamediterraneo.com/forum/topic.asp?TOPIC_ID=233502).

Specimen MCSN8458 (Embiodea) is the most ancient record of this group, for which so far the oldest known fossils have been described by Huang and Nel (2009) from the Middle Jurassic of Inner Mongolia, China. In general, few fossils of the group are known and mostly from Miocene amber. It shows the swollen basitarsi, which are the more characteristic feature of this group, strictly related to their mode of life. In fact, Embiodea live a gregarious life, dwelling in silk galleries they weave under leaves or bark.

It is perhaps not by chance that two of this records concern two groups, the ordere Embiodea and the family Tingidae, whose internal relationships are still controversial, once more pointing out the importance of the fossil record for phylogenetic reconstructions.

9.3. The paleoenvironmental implications of the entomofauna of Monte San Giorgio

The composition of MSG fossil insect assemblage provides important information on the paleoenvironment.

The entomofauna from Monte San Giorgio includes terrestrial groups, with both phitophagous (Hemiptera, Ommatidae, Embiodea?, Cupedidae?, Orthoptera?) and predatory habits (Trachypachidae), and aquatic groups, collected both as larvae (?Plecoptera) and as adults (Ephemeroptera, ?Coptoclavidae).

Coleoptera are the most represented order with six specimens, both whole individuals (three) and fragments (three). The relative high abundance of beetles remains, and in particular the occurrence of fragments and isolated elytra, could suggest a contribution of long term transportation with selective preservation of more sclerotized taxa and parts.

Among terrestrial groups, Trachypachidae are predators and modern representatives of the group (Trachypachinae) dwell in loose soils in definitely terrestrial habitats (Schull et al. 2001). The collected ?Orthoptera and Hemiptera are terrestrial and the extant representatives of the groups are typically phytophagous.

Aquatic forms are also well represented. Seven specimens (adults and larvae) have been assigned to aquatic groups, namely Ephemeroptera (*Tintorina meridensis)*, ?Plecoptera and aquatic Coleoptera (?Coptoclavidae).

All these taxa need permanent fresh water pools or small streams to spend at least one of their developmental stage which, in extant Mayflies (Ephemeroptera) and Stoneflies (Plecoptera), can last for up to three years (Grimaldi and Engel 2005).

Archaeognatha are represented by the two giant MCSN8463 and MCSN8466. Modern Archaeognatha prefer damp environments and may be found under the bark of trees, in soil or leaf litter or in rock crevices. Some species even inhabit rocks at the base of coastal cliffs while others favour rainforest environments. Bechly and Stockar (2011) propose that *Dasyleptus triassicus* was not aquatic, but a terrestrial coast dweller at marine estuaries and the banks of freshwater bodies and swamps.

Interestingly Blattodea,which are the most abundant and diverse group in the main Triassic insect assemblages(Anderson et al 1998; Mancuso et al 2007; Shcherbakov 2008), are absent from our assemblage. Such a pattern was recorded only from “ecozone 6” of the Molteno Formation (Carnian), where horsetails were the dominant vegetation (Anderson et al. 1998).

Taking into account all the taphonomic and environmental elements, a possible scenario is that of a land at a close distance from the depositional basin with ponds or small lakes,some of them permanent, connected to and through a riverine system.At least in the rainy season floodings could bring fresh water dwellers such as estherids and insect larvae to the basin.The emerged lands supporting those fresh waters were probably not too far, allowing for some of the terrestrial insectsto fall into the lagoon to be preserved almost intact. The land probably also supported woods forming at least a loose organic matter rich soil, constituting the living environment for terrestrial insects with predatory and phytophagous habits. The complex paleoenvironment of the Monte San Giorgio area that is coming into light at least for the Late Ladinian time, may probably explain the relatively high biodiversity for the fish assemblage of the Kalkschieferzone. Actually, fish species (more than 20 across the Kalkschieferzone) outnumbered other aquatic macroorganisms such as marine reptiles (1 species) and crustaceans (2-3 genera), so far no molluscs or echinoderms having been recorded from the Kalkschieferzone itself.

9.4. Exceptional preservation

Six of the 16 specimens under study and so far collected from val Mara site D are preserved through phosphatization. Five of them are completely phosphatized and one is partly phosphatized.

In the Kalkschieferzone, phosphatization allowed the preservation of structures, such asparts of the central nervous system and the nervous cord, as well as the Malpighian tubes, that adds to these fossils a significance that goes even beyond their taxonomic importance.

Preservation of the nervous system in compression fossils is so far known only from the early Cambrian Chengjiang biota (Cong et al., 2014; Ma et al. 2012; Tanaka et al, 2013) and in one case in the Burgess Shale fauna (Strasfeld et al, 2011).

The occurrence of phosphatization in only some of the specimens makes the question arise on which factors were playing a role in determining the type of conservation. It must be noted that phosphatization in the Kalkshieferzone occurrs only in arthropods, both insects and crustaceans and has never been observed in vertebrates.

Three main factors can be evaluated, namely:

- the specific conditions of the depositional environment
- the characteristics of the chitin (specific composition and degree of sclerotization)
- the degree of decay of the animal at the moment of burial and fossilization.

The conditions of the depositional environment were probably similar during time: an anoxic, possibly hypersaline environment, though a seasonal variation can be supposed. The only macroscopic difference could be represented by a different input in organic matter, as recorded by the color of the substrate. In fact, the Kalkschieferzone is often characterized by finely laminated beds recording 'seasonal' alternation at the permanent anoxic bottom of the marine basin, possibly influenced by cyclical climatic changes. Light layers are believed to have been deposited during the dry "summer" and dark layers during the "winter" rainy season (Tintori 1990). All the five phosphatized specimens have been found on the darkest surfaces, as three other enigmatic abdomens which are not unequivocally identified as insects and therefore have not been included in this study. Unfortunately, there are exceptions to this rule. The non phosphatized specimen *Praedodromeus sangiorgensis* comes from a dark layer; MCSN 8456, the only specimen which is partially phosphatized, and *Tintorina meridensis* paratype are found on a surface of intermediate color

Notocupes was not available for comparison.

Concerning the group-specific composition of chitin, it can be observed that phosphatization has occurred in hemimetabolous insects, ?Orthoptera, ?Plecoptera and Embiodea and in the "apterygote" Archaeognatha. It is possible that chitin composition is different in these taxa or that the degree of sclerotization is lower. This last case is ascertained for Archaeognatha and plecopteran larval stages. Unfortunately, information on chitin composition and on its alteration/degradation/dissolution after the animals death is scarse.

The degree of decay of the carcass reaching the depositional environment might play a major role. In fact, being phosphatization dependent on authigenic phosphate availability (Allison, 1988a and 1988b; Briggs et al, 1993; Gabbott et al, 1995;Gall, 1990; Orr et al, 2008; Wilby and Martill, 1992), well preserved soft tissues must be a prerequisite for it to take place. It should be hypothesized that the insect reached the bottom of the depositional basin very quickly, soon after death, before significant decay could take place. The fact that *Praedodromeus sangiorgensis*, preserved on a dark layer, hasn't undergone phosphatization, could then be due to the degradation of the soft tissues prior to the settling on the bottom of the depositional basin following a more prolonged (subaerial?) decay. On the other hand, all the phosphatized specimens have lost part or all appendages and legs, that normally disarticulate from the carcass only after the soft tissues have decayed.The loss of limbs is apparently in disagreement with the idea that the insect reaches the bottom virtually intact. It is evident that the mechanisms allowing phosphatization in the Kalkshieferzone are quite complex.

It is particularly interesting the state of specimen MCSN8456, where phosphatization occurred while the exoskeleton was made transparent probably by a process of dissolution.

9.2.1 The nervous system.

Specimens MCSN8463 and MCSN8462 preserve structures of the nervous system, providing the objective proof that the hypotheses on the evolution of these structures are correct but also showing the 'modernity' of Triassic insects.

The idealized concept that the insect's ancestor possesses a segmental pervasivity with a perfectly segmented ventral nerve chord, hypothesized on the basis of extant taxa, has been here firstly demonstrated in a ~240 Mo fossil, MCSN8463, by the presence of the segmented four pairs of abdominal ganglia with their connectives matching the abdominal segmentation. Noteworthy, the structures of the optical ganglia highly resemble those possessed by extant insects. These findings, particularly when comparing them with the information from the Chengjiang arthropods (Cong et al., 2014; Ma et al. 2012; Tanaka et al, 2013), suggest that the evolution of new selectively advantageous structures/functions could occur in relatively short amount of time followed by long period of stasis.

9.2.2 The Malpighian tubes.

Specimens MCSN8462 and MCSN8457 preserve the Malpighian tubes.The preservation of Malpighian tubes has yet never been previously reported in any of the fossil insects. They are part of insects excretory and osmoregulatory system and consist of branching tubes extending from the alimentary canal. Beutel et al (2014) report how they particularly numerous in some polyneopteran groups: we found a significant mass of Malpighian tubes in specimen MCSN8456, an unidentified polyneopteran.

9.5. Gigantic Size

The size of three of the specimens under study, the Archaeognatha and the Tingidae, are out of the dimensional range of the known extinct and extant species. The longest known Archaeognatha (including †Monura) is approximately 20 mm long while MCSN8463 is approximately 40 mm long. So far, the biggest known Tingidae is approximately 8 mm long, while most extinct and extant species fall within a length of 5 mm: MCSN8459 is 11 mm long.

In the Paleozoic, insects reached considerable dimensions. An explanation has been sought in the higher concentrations of atmospheric oxygen, but the hypothesis requires confirmation.

Chown and Gaston (2010) reviewed the state of the art on the subject, identifying several groups of factors that play a role in influencing the size of adult insects. They include physiologic constraints, ontogenetic and phylogenetic variation, intraspecific variation and evolutionary and ecological trends influencing size variation through time. It has not yet been investigated which factors are the object of selection.

An important outcome from the several experiments and observation carried out is that oxygen concentration alone cannot account for gigantism (Okajima, 2008; Clapham and

Karr, 2012). In fact, Po_2 increased also during the Cretaceous but gigantism did not arise, at least in insects, with the exceptions of the mayfly family Hexagenitidae (Dudley, 2000). Physiologic and anatomic constraints, deriving from the structure of the tracheole, limit insects in the adaptation to a greater availability of oxygen (Kaiser et al., 2007).

Climatic conditions can be related to species size variation, also indirectly influencing trophic resources availability. It has been observed in recent forests that dramatic changes in vegetation structure cause firstly the loss of the largest species, probably more sensitive to changes in resource availability (Steencamp and Chown, 1996; Coetzee, van Rensburg and Robertson, 2007). Higher temperatures could lead to the rapid growth of smaller individuals (Davidowitz et al, 2004; Davidowitz and Nijhout, 2005). However, if the climate is very favorable, species can switch from univoltine to multivoltine, thus reaching reproductive stage at a smaller size (Koslowski et al, 2004).

All authors point out that flying insects should be particularly susceptible to variations in atmospheric P_{O2} because of the high energy demands of their flight musculature. As most of the studies are related to flying insects, the variability of global parameters and/or regional climate influx on apterygota such as the Archaeognatha, by far our largest insect, is unknown. It seems probable that the Late Ladinian climate, which is considered to have been monsoonal, wouldn't provide the optimal condition that could trigger the shift to multivoltine reproduction. Thus, even if the temperature was favourable, being the region subtropical, less mobile species, as Archaeognatha and Tingidae, could be 'negatively' affected by the environmental conditions during the rainy season, allowing specimens to continue growth.

An important influence can also be played by predation pressure: when strong, it would favor smaller, less conspicuous specimens. Chown and Gaston (2010) report that the largest recent insects (extant or recently extinct) either typically spend the bulk of their lives as concealed feeders (e.g. beetle species in the Cerambycidae, Scarabaeidae, Dynastinae) or are restricted to oceanic islands where predation pressure may be lower (e.g. St Helena giant earwig *Labidura herculeana*, New Zealand giant weta *Deinacrida* spp.). The fact that both our 'giants' are no-flying or mainly ground/tree dwellers, could be at least partly explained by the absence of ground predators on the small islands or larger emerged lands surrounding the Kalkschieferzone basin. Unfortunately, not enough information is available on the terrestrial environment of Monte San Giorgio to estimate the impact of predation, andso far no other terrestrial animals such as anphibians and small reptiles have been found in the Upper Ladinian rocks from Lombardy, although we must suppose there were some (Tintori, personal communication).But noticeably Liebherr (1988) points out that phyletic size increase among the 34 groups of Coleoptera examined in his work it’s associated with brachyptery.

Taken all these elements into account it is not possible to draw a definitive conclusions on the causes for the anomalous size of these two taxa,nor to evaluate whether this entomofauna was generally subject to the development of gigantism.

9.6. Biostratinomy

The degree of preservation critically depends on the state of the insect reaching the bottom, where it undergoes burial and fossilization. Martinez-Delclòs et al. (2004) remark that floating time is longer for insects that diein subaerial medium, while it's shorter for insects falling alive in the water: as the insect struggles to escape and rise again from the water surface, more water penetrates into its body. During the floating time, insects can undergo a series of processes mainly related to predations (by fishes, amphibians and other insects), transport and decomposition.

Predation can be selective in many regards and may produce fragments with different floating potential (Martinez-Delclòs et al, 2004), or it can cause disarticulation and selective preservation. Predation can occur through all the water column, apart from layer where conditions are too adverse (for instance hypoxia/anoxia, extreme salinity), while chemo-bacterial decomposition takes place in the oxygenated layers and, though slower, also in anoxic environments.

Terrestrial insects preserved in aquatic environments are surely allochthonous. Therefore, in case they are disarticulated or preserved as isolated fragments (more often wings or coleopteran elytra), there are three possible explanation for this conservation (Mancuso et al, 2007):

1) They reached the water body already disarticulated for both decay or predation
2) Insects were selectively preyed when in the water and only wings were left to be preserved
3) They suffered decay to a variable extent staying at the water surface or during a very slowsinking to the bottom.

Mancuso et. al (2007), analyzing the fossil assemblage of Los Rastros Formation, remark how the preservation of whole insect bodies indicates that the specimens reached water alive or at least intact and sank rapidly, reaching theanoxic and therefore undisturbed bottom where they were rapidly buried.

The same pattern can be recognized in some of the specimen under study, where the insect has been preserved whole but a closer examination reveals that legs (and elytra, for coleoptera) are slightly displaced or were disarticulated at the insertion into the body and were moved from their original position at the time of deposition. In one instance (MCSN8455), the fragment of a leg is preserved at approximately 1 cm from the rest of the body. The paratype of *Tintorina meridensis* (Krzeminski and Lombardo 2001) is preserved as isolated wings and a thorax segment, while the holotype of *Tintorina meridensis* (MCSN4666) is missing the head and the anterior part of the abdomen. Specimen MCSN8466is preserved, phosphatized, only from the metathorax to the end of the abdomen but has lost all appendages, cerci included.

Duncan et al. (2003) realized a series of experiments on decay, transport and breakage, and observations on the main types of predators, to explain the phenomenon of wing dominance in fossil blattoids, from which a vast record from the Carboniferous deposits is available. The experiments were performed on entire cockroaches either asphyxiated and then transferred in artificial fresh water or thrown alive into the water. The artificial fresh water used was inoculated with water from an environment capable to best simulate the conditions of the carboniferous depositional environment. The decay experiments were monitored at two week intervals for up to 58 weeks and changes in the degree of decay/disarticulation were noted, recording the internal and external state of the carcasses as well as the presence of fungal growth and bacterial films on the emergent carcasses and vessel bottoms. Their results are summarized in fig. 27. After death, the carcass is floating on the surface, ventral side down. Decay starts from internal organs that liquefy. Then muscles and fat tissue degrade to a white, semi liquid state. The carcass then becomes flaccid while still retaining its integrity and minor ruptures between tergites may appear. First cerci and then antennae disarticulate, and eyes collapse. Finally the abdomen begins to disintegrate and the carcass reaches the bottom. In this process, disarticulated parts can detach, thorax and head being the more resistant. Forewings and finally hindwings are the last to become loose. The time required for the whole sequence to take place can reach 30 weeks in still waters but only 70 hours in running waters. When comparing the state of preservation of the fossils under study with this sequence, different cases are met:

- *Tintorina meridensis* holotype is lacking the head and the last abdomen segments: it could have floated or been transported for an intermediate time before setting to the bottom.
- Beetle fragments are obviously the remains of a long process of decay, that could have taken place at some distance from the depositional point, even on emerged land, allowing the preservation of only the most sclerotized fragments.
- The phosphatized specimens preserve internal organs and soft tissue structures, and therefore reached the sediment shortly after death and must have dwelled in

proximity of the basin. However, flying insect could be transported above the water by the wind when still alive.

All these elements point to a double origin of the fossilized insects: the phophatized specimens probably lived in the proximity of the depositional basin, that was reached short after death or while still living. The fragmented specimens probably lived farther away from the depositional basin and underwent some subaerial decay before reaching it, in a few cases for a relatively long time(elytra and abdomen fragments). The specimens which appear whole but are not phosphatized, and that lost head appendages and some or all their legs, can be hold to represent an intermediate situation, either relative to the distance of the living habitat or of the decay time in subaerial or aquatic environment.

It must be noted that *Tintorina meridensis*, a mayfly, and MCSN8455, an aquatic fresh-waters beetle, according to the previous considerations, would have lived at some distance from the depositional basin.

A comparison of the findings of whole insects between MSG and the more important Triassic sites however highlights that this percentage is significantly higher in MSG, amounting to 75%.

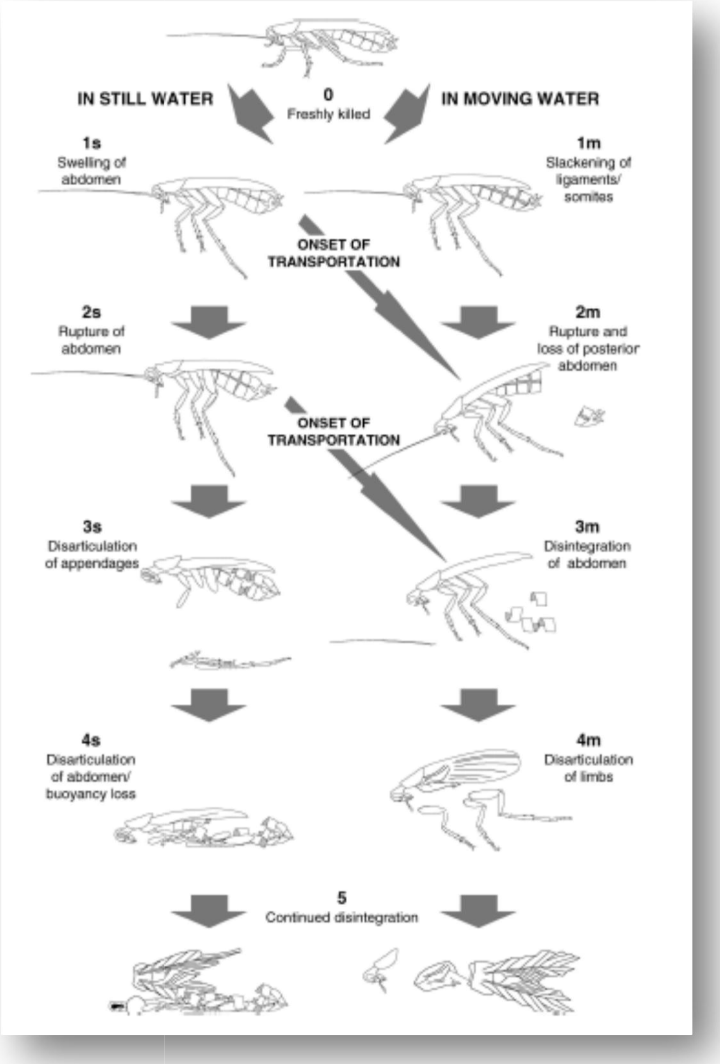

Fig 27: stages of decay in insects after deployment in still or moving waters. From Duncan et al. (2003)

10. ***Conclusions***

The study of the entomofauna of the Kalkschieferzone of Monte San Giorgio has proved to be a real challenge.

The first aim of this research, the identification of all the specimens, has been fulfilled to the extent to which the degree of preservation allowed.

The state of preservation and the type of conservation were at the same time a problem and a great surprise. Many specimens are only apparently well preserved but at a closer examination, required to carry out a consistent diagnosis, the main diagnostic features were found to be missing. A typical example is specimen MCSN 8456, that could be defined 'beautiful to see' but that hasn't been assigned to any order. It must be said that it is also possible that it represents a form of transition inside the Polyneopteran superorder, among which orders in the Triassic evolution was at work.

This assemblage has provided some of the oldest fossil records for four orders: Trachypachidae and Ommatidae (*Notocupes* sp) among Coleoptera; Archaeognatha; Tingidae among Hemiptera; Embiodea. This is definitely an important contribution in filling some of the gaps in the paleontologicalinsects evolution.

It cannot be excluded that further study with more refined observation techniques on the more undetermined specimens could provide new information and allow their definitive identification.

These findings remark how our hypotheses on taxa evolution are hindered by the gaps in the fossil record. These gaps are particularly important for terrestrial taxa, as most insects are, for which the conditions for preservation are rarer than aquatic ones.

Concerning the second aim of this research, to increase the information on the Monte San Giorgio paleoenvironment, progress has been made through the identification of groups colonizing very diverse environments: fresh water permanent basins (Ephemeroptera), leaf litter and loose soils (Trachypachidae, Embioptera, Cupedidae, Ommatidae), vegetation (Orthoptera, Tingidae), confirming a much more complex environmental setting than a carbonatic platform. Both fresh water and emerged land must have been permanently available.

Another exceptional feature of this assemblage is represented by preservation through phosphatization. Phosphatization allowed access to anatomical structures that have been preserved only twice before in compression, in Chengjiang and in one instance among the Burgess Shale fossils, and never in the Mesozoic.

The phosphatization of structures of the nervous system is so exceptional that appoints to these fossils a significance that goes beyond the mere systematics.

Therefore, the results of this PhD research patently highlight the exceptionality of this fossil assemblage.

There is no indication that the excavation of the locality D in Val Mara, near Meride (Canton Ticino, Switzerland), but also site VM 227, brought to light all the fossils they could yield, given also the fact that excavations were aimed mainly to the research of vertebrate fossils, for which Monte San Giorgio Triassic lagerstätte is famous.It is highly probable that more fossil insects are to be recovered and, possibly, more phosphatized specimens from locality D, specimens so important to give us new information on the internal morphology of insects in the Triassic.

The exceptionality of their fossil record, more so since it comes from the Mesozoic period and specifically from the Triassic, a crucial period to understand recovery from the Permian/Triassic crisis event, demands that field activities should start again.

To neglect this opportunity, avoiding to take action,would determine the loss of crucial information in the evolutionary history of insects, which is in turn strictly related to the evolution of the environmental conditions. Moreover, the information provided by these fossils is also important in the calibration of phylogentic reconstructions based on nuclear data, allowing the reduction of uncertainty in chronograms, with consequences that reach further than the knowledge on the specific group.

Finally, in 2003 Monte Sang Giorgio having been ascribed in the UNESCO World Heritage List for its fossil fauna, it must be sadly remarked that so far no action to bring this mission in evidence and to give value to this heritage.

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Appendix 1

Strada, L., M. Montagna, and A. Tintori (2014). A new genus and species of the family Trachypachidae (Coleoptera, Adephaga) from the upper Ladinian (Middle Triassic) of Monte San Giorgio. Rivista. Italiana di Paleontologia e Stratigrafia. 120, 183–190.

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A NEW GENUS AND SPECIES OF THE FAMILY TRACHYPACHIDAE (COLEOPTERA, ADEPHAGA) FROM THE UPPER LADINIAN (MIDDLE TRIASSIC) OF MONTE SAN GIORGIO

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Key words: Fossil Insects, Trachypachidae, new genus and species, predator, Middle Triassic, paleoenvironment.

Abstract. A new genus and species of fossil Trachypachidae *Pseudodromeus sangiorgiensis* gen. n., n. sp. (Coleoptera, Trachypachidae, Eodromeinae), with well developed asymmetrical mandibles, shorter than the head, subrectangular pronotum and slender tibiae, longer than femora, is described from the Kalkschieferzone (uppermost member of the Meride Limestone) of the Swiss side of Monte San Giorgio. Trachypachidae are terrestrial Coleoptera well represented in the Mesozoic fossil record by the extinct family Eodromeinae. Up to now, more than 33 fossil species belonging to 13 genera of Eodromeinae have been described. The new species is part of a collection of fossil insects that includes members of at least six different orders. Based on the ecology of corresponding extant taxa, this insect assemblage provides new insights on the paleoenvironment of Monte San Giorgio area during the Late Ladinian. The assemblage includes terrestrial taxa that support the presence of emerged land and taxa with long-lasting aquatic larval stage (as Plecoptera and Ephemeroptera) that confirm the presence of stable fresh water basins.

Introduction

Monte San Giorgio is a fossil Lagerstätte known since the 19th century due to industrial exploitation of bituminous shales as well as for the numerous paleontological excavations that took place mainly in the last century. In time, it has yielded several remarkable fossils of marine fishes and reptiles as well as invertebrates and terrestrial plant remains. Lying across the Italian-Swiss boundary to the South of the Ceresio Lake (Fig. 1), this area is now in the World Heritage List of UNESCO for its global paleontological meaning of its marine vertebrate faunas.

Regarding the Kalkschieferzone, top of Meride Limestone, dated Late Ladinian, 240 – 239 Ma following Stockar et al. (2012), it was so far renowned for its vertebrates, mostly fishes but also a few reptiles (Lombardo 2001; Renesto et al. 2003; Tintori 1990a; Tintori & Lombardo 2007). However, also arthropods, such as conchostracans (Tintori 1990b; Tintori & Brambilla 1991) and mysidaceans (Larghi et al., submitted), are important in the Kalkschieferzone fossil assemblages.

During the fieldwork carried out between 1997 and 2003 in the Lower Kalkschieferzone at the Val Mara site D near Meride, about 16 specimens of insects (both adult and larval forms) have been collected. Only two specimens have been so far described as a new genus and species of Ephemeroptera (Krzeminski & Lombardo 2001). In the same paper, Krzeminski & Lombardo (2001) described also a specimen of *Notocupes* (Coleoptera, Ommatidae) from the Lower Meride Limestone. Recently, a new species of Dasyleptidae (Archaeognata) from the Upper Kalkschieferzone was described by Bechly & Stockar (2011). These findings make the Kalkschieferzone of Monte San Giorgio a unique site for Middle Triassic insects.

We herein describe a new species and genus of Eodromeinae (Coleoptera, Trachypachidae). Trachypachydae includes the single extant subfamily Trachypa-

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Fig. 1 - Val Mara site D - geographic position.

chinae (two genera described: *Trachypachus* and *Systolosoma*), for a total of six species (Maddison et al. 2009) and the extinct subfamily Eodromeinae (Ponomarenko 1977). Eodromeinae is well represented in the fossil record from the Triassic to the Cretaceous and it is much more diverse than Trachypachinae (Ponomarenko 1991). At present, at least 33 fossil species belonging to 13 genera of Eodromeinae have been described (Ponomarenko 1977; Soriano et al. 2007; Hong 1983; Jin & Ren 2011; Wang et al. 2012; Ponomarenko & Volkov 2013). The oldest genera are from the Terminal Permian (Ponomarenko & Volkov 2013) and only one other genus (*Sogdodromeus* Ponomarenko, 1977) is from the Triassic (Ponomarenko 1977). Also, during our preliminary survey on this insect collection, the undescribed specimens were tentatively assigned to six orders namely Ephemeroptera, Orthoptera, Plecoptera, Embioptera, Hemiptera and Coleoptera. Based on the current knowledge about the ecology of these orders, based on both extant and fossil species, we provide new insights on the paleoenvironment of Monte San Giorgio at least during the Late Ladinian.

Insect taphonomy

The specimen under study preserves the general layout of the body. Nonetheless, body segments and legs, and to a lesser extent, head parts and abdomen are displaced from their anatomical position in the living animal. This layout suggests that the specimen went through a first stage of decay in subaerial and/or superficial aquatic environment, during which soft tissues partially degraded. Therefore, either the insect died and partially decayed on the ground, its original habitat, and was then transported by a 'high' energy event, such as a flood following heavy rains or just wind, to the depositional basin. Alternatively, it fell directly on the water surface while flying, floated for some time undergoing a rapid initial decay in the warm superficial waters before sinking to the bottom, where burial and fossilization then took place. Moreover, since floating insect remains are subjected to predation, they were probably transported only for short distances. The time lag between death and burial determined the extent of soft tissues decay: when the body reached the bottom and possibly, during initial post-burial compaction of the sediment, the disarticulation became apparent. In the specimen, the body layout is preserved so we can infer that decay was time limited and the depositional environment was without any current that could help in the dispersal of the somewhat loose body parts.

The degree of conservation of the other specimens varies greatly, probably recording strong variations in the taphonomical history. In a few instances, only head, thorax and abdomen outline is preserved, while in other cases also appendages remained. In almost one-half of the fossils soft tissues preservation occurs, probably due to a phosphatization process, sometimes preserving internal structures in detail.

Material and methods

The specimen has been collected in locality D in Val Mara, near Meride (Canton Ticino, Switzerland) and is deposited at Museo Cantonale di Storia Naturale di Lugano (MCSN). Specimen manipulation and measures were completed with the auxiliary use of the stereo microscope Leica M80 and an ocular micrometer. Images were acquired by digital camera Canon Eos 450 mounted on a machinery in order to scan the sample at different focus layers that were mounted with Zerene Stacker 1.0 (Student Edition). Drawings were made with camera lucida attached to the microscope.

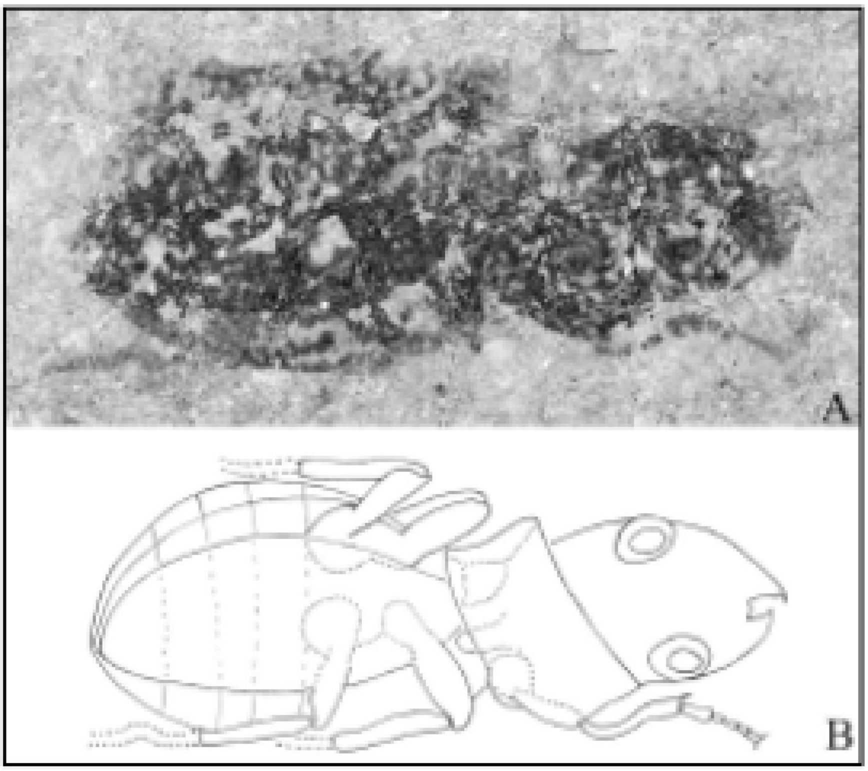

Fig. 2 - A) *Praedodromeus sangiorgiensis* gen. n., sp. n. Length from apex of mandibles to apex of elytra = 10.8 mm. B) drawing of the specimen.

Systematic paleontology

Order **Coleoptera** Linnaeus, 1758
Suborder **Adephaga** Schellenberg, 1806
Family Trachypachidae Thomson, 1857
Subfamily Eodrominae Ponomarenko, 1977
Genus *Praedodromeus* gen. nov.
Type species: *Praedodromeus sangiorgiensis* n. sp. by monotypy.

Etymology: The name derived from the Latin verb *"praedo"*, which means to prey, considering its strong and sharp mandibles that are supposed to be used to catch prey, and the suffix "*-dromeus*", which means "runner", from its cursory legs.

Locus typicus: Site D, Val Mara near Meride, Mendrisio, Canton Ticino, Switzerland.

Diagnosis: The general habitus of the new taxon (genus or species), a simple sulcate antenna cleaner in the distal part of the tibiae, the metacoxa separating the thorax and abdomen, the metaepisternum reaching the meso-coxal cavities prompts its ascription to the to the family Trachypachidae, subfamily Eodrominae. The new taxon is described as new genus and species due to the presence of a unique set of characters: well developed asymmetrical mandibles; rectangular pronotum, longitudinal groove absent; short metaventrite; and big head with large eyes on the upper surface.

Praedodromeus sangiorgiensis sp. n.

Fig. 2A, B

Holotype: MCSN 8451.

Etymology: The name derived from the collecting area of Monte San Giorgio (Switzerland/Italy).

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

Description

Almost complete impression in dorsal view, lacking antennae. Head and abdomen in natural position, single disarticulated elytron preserved. Length from apex of mandibules to apex of elytra of 10.8 mm; width at base of elytra of 4.6 mm (length-width ratio 2.34).

All three legs on the right side preserved. Mid and hind femora rather large and robust; maximum width of right mid femora is 0.79 mm. Tibiae thin and slender. The preserved tarsi (I+II) elongated and slim; only two fore tarsomers distinguishable, first one enlarged. On the left side preserved only II+III femora and III tibia. Right fore tibiae (length 1.92 mm) harbouring a simple sulcate antenna cleaner organ with enlarged distal area and an apical spur (0.24 mm). Five tarsi (total length 1.62 mm) on I right leg clearly visible. Slender tibiae.

Head big, longer than wider, length of 3.0 mm mandibles excluded and of 3.42 mandibles included, width at the eyes 2.76 mm. Mandibles asymmetrical and triangular, robust and sharp with a small teeth in the anterior second-third of the inner margin. Total length of 1.38 mm, width 0.96 mm, length-width ratio of 1.44. Partial impression of labial palp visible between mandibles.

Pronotum wide (3.1 mm), anterior margin slightly concave with pointed apices (left side), posterior margin straight.

Abdomen partially visible with light impressions of segmentation preserved on the left side. Length of abdomen 1.5 times the length of meso- and metathoraces combined.

Discussion

The specimen has been described based on the preserved morphological characters even if some key characters are lacking, probably due to subaereal degradation before burial. Better-preserved features include the general habitus, the mandibles and the very developed head with dorsal eyes. The new genus differs from *Petrodromeus* (Ponomarenko & Volkov, 2013), *Permunda* (Ponomarenko & Volkov, 2013), *Karatoma* (Ponomarenko, 1977), *Sinodromeus* (Wang et al., 2012), *Pseudodromeus* (Ponomarenko, 1977), *Xinbinia* (Hong, 1983) and *Fortiseode* (Jin & Ren, 2011) for the absence of punctuations and/or striae on elytra. The genera *Petrodromeus* (Ponomarenko & Volkov, 2013), *Permunda* (Ponomarenko & Volkov, 2013) and *Karatoma* (Ponomarenko, 1977) show a lower head width/length ratio compared to *Praedodromeus* gen. n. The new genus markedly differs from *Fortiseode* and from *Xinbinia* also for the shape of body, pronotum and head. It also differs from *Sogdodromeus* (Ponomarenko, 1977) in the longer abdomen and in the shape of the pronotum. Compared to *Platycoxa* (Ponomarenko, 1977) it differs in the shape of pronotum and mandibles, in the shorter head capsule and smaller eyes. *Praedodromeus* gen. n. differs from *Unda* (Ponomarenko, 1977) and from *Permunda* (Ponomarenko & Volkov, 2013) in the width and shape of the pronotum, which lacks the pointed anterior margins and is less markedly narrower than the base of the elytra. Compared to *Karadromeus* (Ponomarenko, 1977) the new taxon has legs with longer femora, protruding beyond lateral margins of the body and tibiae longer than femora. The comparison with *Beipiaocarabus* (Hong, 1983) is difficult, since the holotype found by Hong is preserved in ventral view, which we are missing. Anyway, apparently in *Beipiaocarabus* the abdomen is shorter, the metathorax is quite longer and femora are less strong and thick than in *Praedodromeus*.

The Kalkschieferzone insect assemblage and its paleoenvironmental implications

The depositional environment for the Kalkschieferzone is that of a shallow lagoon, adjacent to a carbonatic platform (S. Salvatore Dolomite). Toward West-North/West it faces a deeper basin (Perledo-Varenna Formation) and the complex system of carbonatic platforms of the Esino Formation further to the East, with somewhat limited connection to the open and deeper sea (Tintori 1990a; Tintori & Lombardo 1999; Lombardo et al. 2012). Sedimentation took place below wave base and on an often anoxic bottom, as indicated by common laminated limestone or marly-limestone layers and the almost general absence of bioturbation (Tintori 1990b; Tintori & Renesto 1990; Tintori & Lombardo 1999; Lombardo et al. 2012). Common are also clay-chips beds, often rich also in dark algal-film fragments, probably related to storms affecting the shallower part of the basin or the threshold toward the open waters. The Kalkschieferzone basin was clearly also sometimes affected by sudden fresh water supply following stormy heavy rains, as there is record of several levels rich in conchostracans crustaceans (Tintori 1990a; Tintori & Brambilla 1991). Furthermore, fresh water could induce strong sudden changes in the lagoonal environment originating mass mortality events among marine fishes (Tintori 1990a; Lombardo et al. 2012) aggravating the general water conditions thus causing abortion in the marine reptile *Lariosaurus* pregnant females (Renesto et al. 2003). The fresh-waters flowing above the salted ones could also induce a temporary water stratification, preventing a general mixing. This made the lower water layer less and less oxic due to the organic matter decay at the bottom. As terrestrial dwellers, insects were probably less affected by such events: however, storms could have thrown the insects over the basin itself.

We have identified 13 still undescribed specimens as belonging to six different orders: Ephemeroptera, Orthoptera, Plecoptera, Embioptera, Hemiptera and Coleoptera. They include both terrestrial and aquatic forms, the latter as adult and larval stages. Here we consider as aquatic the insect groups that require an aquatic environment during at least one developmental stage.

Table 1 shows the list of the identified taxa, the number of specimens for each taxon and their living environment, based on the assumption that the living environment of fossil groups can be inferred from that of extant representatives. Two more specimens remained unidentified.

Six specimens, belonging to four different orders, are terrestrial: they include Orthoptera, Embioptera and, among Coleoptera, Trachypachidae and Cupedidae? In addition, the morphological features of the two Hemiptera specimens are closer to those of terrestrial families than to those of aquatic ones. Among terrestrial groups, Trachypachidae are predators and modern representatives of the group (Trachypachinae) dwell in loose soils in definitely terrestrial habitats (Schull et al. 2001). The Orthoptera and the two Hemiptera collected are terrestrial and the extant representatives of the groups are typically phytophagous.

Within the fossil insects of Monte San Giorgio, aquatic forms are well represented. We have assigned seven specimens (adults and larvae) to aquatic groups, namely Ephemeroptera (among these, *Tintorina meri-*

Order	**Family**	**Species**	**N° of specimens**	**Living environment**
Ephemeroptera	Tintorinidae	*Tintorina meridensis*	2 (adults)	Strictly freshwater for reproduction and life through all the immature stages; in clean still or running waters. Larvae food on plant or, more rarely, animal debris
Ephemeroptera	nd*	nd*	1 (nymphal stage)	Strictly freshwater for reproduction and life through all the immature stages; in clean still or running waters. Larvae food on plant or, more rarely, animal debris
Orthoptera	nd*	nd*	1	Preferentially terrestrial habitats although some species live on the shores of ponds, streams, lakes, and rivers phytophagous, otherwise carnivorous/predatory
Plecoptera	nd*	nd*	2 (1 adult, 1 nymph)	Freshwater, clean, cold and running waters. Phytophagous or predatorial habits
Embioptera	nd*	nd*	1	Strictly terrestrial and phytophagous; feeding on leaf litter, moss, bark and lichen. Subsocial behavior, can build tunnels and chambers woven from the silk they produce on rocks and the bark trees, or in leaf litter
Hemiptera	nd*	nd*	2	Terrestrial, phytophagous or parasitic
Coleoptera	Trachypachidae	*Praedodromeus sangiorgiensis*	1	Strictly terrestrial habitat, both in the larval and adult stage, with predatory habits, extant species (Trachypachinae) dwell in loose soils
Coleoptera	Cupedidae?	nd*	1 (elytron, fragment)	Strictly terrestrial. Larvae: wood borers, typically live in fungus-infested wood, feeding on dead, fungi infested wood. Adults live in dead subterranean wood such as tree roots, buried structural timber and the rotten cores of living trees or stumps
Coleoptera	Coptoclavidae?	nd*	1 (adult)	Freshwater. Predatory habits
Coleoptera	nd*	nd*	1 (abdomen fragment)	nd*

Tab. 1 - Fossil assemblage and environmental features. **Note: n.d = not determined*

densis), Plecoptera and aquatic Coleoptera (Coptoclavidae?). All these taxa need permanent fresh water pools or small streams to spend at least one of their developmental stage which, in extant Mayflies (Ephemeroptera) and Stoneflies (Plecoptera) can last for up to three years (Grimaldi & Engels 2014).

Interestingly Blattodea, which are the most abundant and diverse group in the main Triassic insect assemblages (Anderson et al 1998; Mancuso et al 2007; Shcherbakov 2008), are absent from our fossil assemblage. Such a pattern was recorded only from "ecozone 6" of the Molteno Formation (Carnian), where horsetails were the dominant vegetation (Anderson et al. 1998). Bashkuev et al (2012) have described the fossil insect assemblage from the Upper Buntsandstein of Lower Franconia and Thuringia, dated Anisian, including more than 300 specimens, where coleoptera represent from 48 to 78% of collected material but Blattodea are also present.

Regarding the life environment of the Kalkschieferzone insects, the emerged land during the Late Ladinian in the Monte San Giorgio area has never been precisely recorded, though some fresh waters had to be supposed owing to the presence of conchostracans (Tintori 1990b). The San Salvatore Dolomite surrounded the Meride Limestone basin(s) and possibly had small temporary islands as already supposed by Tintori (1990b), Krzeminski & Lombardo (2001) and Bechley & Stockar (2011). Presence of Ephemeroptera (Krzeminski & Lombardo 2001) and Dasyleptidae (Bechley & Stockar 2011) specimens points to a quite close source area especially if we consider that the three specimens of *Dasyleptus triassicus* have been found on a single mass mortality surface (Lombardo et al. 2012). This means that the transport had not to be long otherwise a much larger scattering of the specimens would have taken place.

The only other record of land dwellers for the Meride Limestone regarded the plants (Stockar & Kustatscher 2010), even if the authors did not give a paleoenvironmental interpretation of the land from where the plant remains came from. Stockar & Kustatscher (2010) only wrote about a possible 'arid' environment quite far from the basin. However, we have also to keep in mind that the flora described by Stockar & Kustatscher (2010) refers to the Cassina Beds, thus at the top of the Lower Meride Limestone, when the general paleoenvironmental conditions were probably different from those of the Kalkschieferzone. So far, only marine dwellers, other than the terrestrial plants and a single insect fragment (Krzeminski & Lombardo 2001), have been found in the lower Meride Limestone compared to the sometimes common esterids (Tintori 1990b; Lombardo et al. 2012) in several horizons of the Lower and Middle Kalkschieferzone. The only similarity between the Kalkschieferzone and the Lower Meride Limestone

Vertebrate levels is the presence of more marly limestones, usually laminated and richer in organic matter. Thus, the preservation windows seem to be related to a higher clay content than in the well bedded limestone that makes up most of the lower and middle Meride Limestone. Which is the origin of the clay and in which way it is related to bottom conditions favorable to nice preservation is still to be analyzed.

The Kalkschieferzone is often characterized by finely laminated beds recording seasonal alternation at the anoxic bottom of the marine basin, influenced by continental areas. Light layers are believed to have been deposited during the dry "summer" and dark layers during the "winter" raining season (Tintori 1990a). A comparison of the surface color on which the insects are preserved prompted us to assign adult stages of aquatic taxa (Coptoclavidae?, Plecoptera, Ephemeroptera) mainly to the "summer" dry season (light laminae). The larval stages (Ephemeroptera, Plecoptera) are assigned mainly to the "winter" rainy season (dark laminae), indicating they were present through the whole year, as were the permanent fresh water basins.

Conclusions

The new taxon is one of the oldest genera of Trachypachidae described so far. Recently, Ponomarenko & Volkov (2013) described two new genera from the terminal Permian of Babii Kamen', Kuznetsk Basin, Siberia. The other Triassic genus, *Sogdodromeus* (Ponomarenko, 1977), comes from the Madygen Formation (Kyrgyzstan), dated Early Carnian (Scherbakov 2008), albeit Scherbakov suggests a Late Ladinian age, based on the fossil insect fauna primitive characteristics. Papier and colleagues (2005) described the beetles collection from Grès a Voltzia, the fossil lagerstätten from the Anisian locality in the Vosges, France. One of the specimens (Papier & al. 2005, p.187, sp. 31, fig 7A) can be recognized as a Trachypachidae, although its systematic position was not stated. *Praedodromeus* gen. n., collected in Southern Europe, therefore expands the range of distribution of Triassic Trachypachidae to the west and contributes to support the idea that the high diversity observed in the Trachypachidae fossil records from Jurassic to Cretaceous could have started during the Middle Triassic.

Of the extant genera of Trachipachydae, *Trachypachus* inhabits the Holoarctic region and *Systolosoma* the Neotropical region (Grimaldi et al. 2004). Trachypachidae fossil record from the Triassic to the Cretaceous is more abundant in Laurasia, but specimens have been described from the Australia Tralbagar fossil fish bed (Beattie & Avery 2012) and from the Cretaceous of the Santana Formation, Brazil (Maisey 1991).

Evans (1982) suggests that Trachypachidae were predators or xylomycetophagous. Ground cover from vegetation was scarce, and beetles were fast runners in order to run across the bare areas without incurring in predation. This hypothesis fits well with *Praedodromeus* gen. n. general habitus, which appears slender and agile, with long, thin cursory legs. Mandibles are well developed and appear apt to predation, eyes are of great dimensions. The new genus does not resemble the more ancient genera *Petrodromeus* (Ponomarenko et Volkov, 2013), *Permosynda* (Ponomarenko et Volkov, 2013) and *Sogdodromeus* (Ponomarenko, 1977), and appears more similar to the Jurassic genera *Karatoma* (Ponomarenko, 1977) and *Karadromeus* (Ponomarenko, 1977) and in general to the Carabids habitus.

Taking into account all the taphonomic and environmental elements, a possible scenario at a close distance from the depositional basin is that of a land with ponds or small lakes, some of them permanent that were connected to and through a riverine system. At least in the rainy season floodings could bring fresh water dwellers such as estherids and insect larvae to the basin. The emerged lands supporting these fresh waters were probably not too far, allowing for the terrestrial insect specimens falling into the lagoon to be preserved almost intact. The land probably also supported woods forming at least a loose organic matter rich soil to form the living environment for terrestrial insects with predatory and phytophagous habits. The complex paleoenvironment of the Monte San Giorgio area that is coming in the light at least for the Late Ladinian time, may probably explain the high biodiversity for the fish assemblage of the Kalkschieferzone. Actually, fish species (more than 20 across the Kalkschieferzone) outnumbered other aquatic macroorganisms such as marine reptiles (1 species) and crustaceans (2-3 species), so far no mollusks or echinoderms having been recorded from the Kalkschieferzone itself. This must be taken into account when comparing the vertebrates faunas across the Tethys after the recent discovery of several Middle Triassic vertebrate sites in Southern China (Jiang et al 2009; Tintori et al. 2013a, 2013b), especially when comparing sites of similar age such as the Xingyi (Guizhou Province, China) and the Kalkschieferzone faunas, both dated to the Late Ladinian (Ji et al. 2012; Tintori et al. 2013).

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