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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Abstract. A new genus and species of fossil Trachypachidae *Praedodromeus 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 mysidiaceans (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 Bechley & 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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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; Jia & 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 MS5 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) *Preadodromeus sangior-giensis* gen. n, sp. n. Length from apex of mandibules to apex of elytra = 10.8 mm. B) drawing of the specimen.
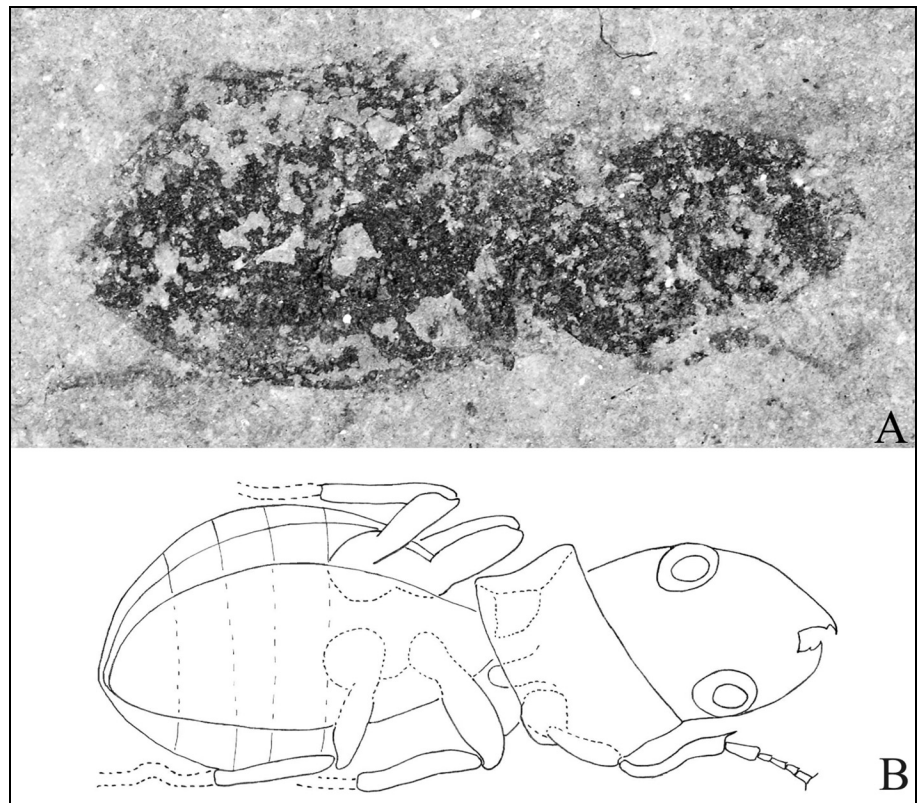
Systematic paleontology

Order **Coleoptera** Linnaeus, 1758

Suborder **Adephaga** Schellenberg, 1806

Family Trachypachidae Thomson, 1857

Subfamily 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 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. 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 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 & Volkov, 2013), *Permunda* (Ponomarenko & Volkov, 2013), *Karatoma* (Ponomarenko, 1977), *Sinodromeus* (Wang et al., 2012), *Psacodromeus* (Ponomarenko, 1977), *Xinbinia* (Hong, 1983) and *Fortiseode* (Jia & Ren, 2011) for the absence of punctuations ans/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, freshwater 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 feed 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 feed 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 (Trachypahinae) 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: nd = 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), indicatimg 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* (Ponomoranko, 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), *Permunda* (Ponomarenko et Volkov, 2013) and *Sogdodromeus* (Ponomarenko, 1977), and appears more similar to the Jurassic genera *Karatoma* (Ponomarenko, 1977) and *Karadormeus* (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 those 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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