

THE MIDDLE TRIASSIC LAGERSTÄTTE OF MONTE SAN GIORGIO REVEALS THE OLDEST LACE BUGS (HEMIPTERA: TINGIDAE): *ARCHETINGIS LADINICA* GEN. N. SP. N.

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Abstract. A new genus and species of fossil lace bugs (Hemiptera; Tingidae), *Archetingis ladinica* gen. n. et sp. n. is described from the Lower Kalkschieferzone (Meride Limestone, Upper Ladinian) of the Swiss side of Monte San Giorgio. The new taxon clearly resembles modern Tingidae in its hemelytra and pronotum, with two rows of areole, in the presence of bucculae closed at the anterior end, not extending beyond the apex of the head, and in the presence of a labial groove on the meso-/metathoracic sternum. Distinctive features are the thick femurs of the first and second pair of legs, the exceptional size (total length of ~12 mm) if compared with both fossil and extant species. *Archetingis ladinica* gen. n. et sp. n. represents by far the oldest known species of this family and brings back the origin of Tingidae of approximately 140 My, well into the Middle Triassic. The discovery of *A. ladinica*, beside its evolutionary consequences on the origin of extant Tingidae, provides evidences for the presence of terrestrial ecosystems nearby to the depositional environment. According to the living and trophic behavior of extant Tingidae, those emerged lands had to be covered by vegetation.

INTRODUCTION

Monte San Giorgio (MSG, Italy-Switzerland) is a Triassic Fossil-Lagerstätte inscribed in the UNESCO World Heritage List for its marine vertebrate faunas, (Felber et al. 2004; Felber 2005). Paleontological researches on MSG date back to the middle of XIX Century, when the first specimens were discovered on the Italian side of the mountain. The unique aspect of MSG is that it concentrates several different fossil vertebrate horizons in a few square km (Felber et al. 2004) covering a time interval from Late Anisian to Late Ladinian. The scientific interest on MSG has been almost always focused on marine vertebrates or on invertebrates dealing with biostratigraphy. More recently, the invertebrates collected from three levels of MSG lagerstätte, among which insects, proved to be of relevant meaning for both paleoenvironmental understanding and evolutionary reconstruction

of these rarely preserved groups of organisms. In spite of the detailed scientific excavations carried out for more than 100 years, the fossil invertebrates have been discovered only recently (Lombardo et al. 1999).

During the fieldwork carried out between 1997 and 2003 in the Lower Kalkschieferzone (Late Ladinian, 239.51 ± 0.15 Ma; Stockar et al. 2012) on the Swiss side of Monte San Giorgio, a remarkably diverse assemblage of 19 insect specimens were collected. The specimens were attributed to six orders and to groups characterized by different ecology and life habits (Strada et al. 2014). So far, seven specimens from this assemblage, ascribed to four taxa, have been formally described: the mayfly *Tintorina meridensis* Krzeminski & Lombardo, 2001, an elytron of the beetle *Notocupes* sp. (Krzeminski & Lombardo 2001), the beetle *Praedodromeus sangiorgensis* Strada et al., 2014 (see also Krzeminski & Lombardo 2001) and a representative of extant bristletail *Gigamachilis triassicus* Montagna et al., 2017. Noteworthy, the entomofauna from the Middle Triassic of Monte

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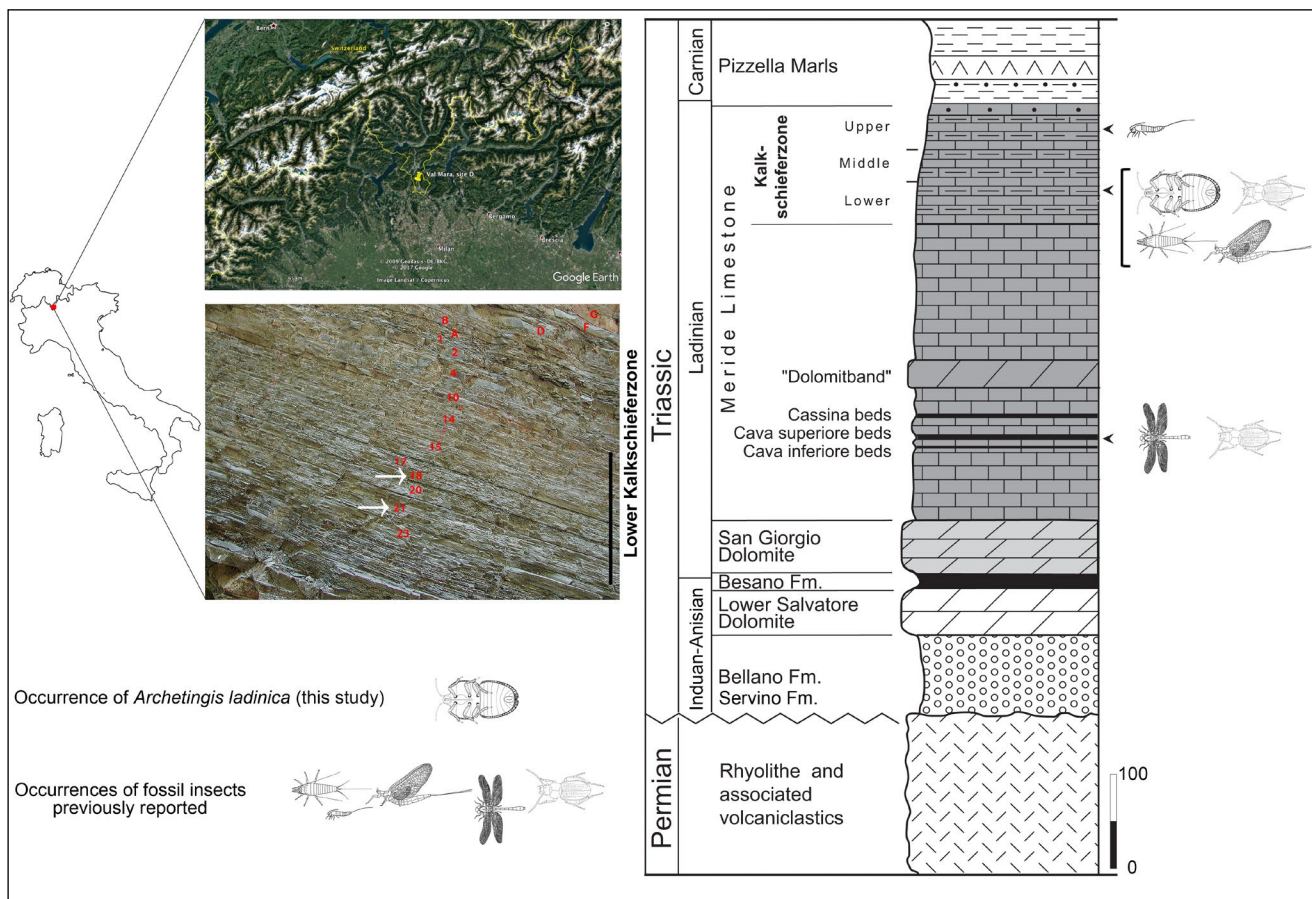


Fig. 1 - Geographic position of the Monte San Giorgio (Italy-Switzerland) UNESCO World Heritage, with the strata of the Lower Kalkschieferzone (Site D Val Mara) excavation from which the specimens were collected (left; indicated by white arrows: *Archetings ladinica* collected from stratum 18 of site D, Val Mara; remnant of *Volzia* collected on stratum 21 of site D, Val Mara; the vertical black bar corresponds to 1 meter) and stratigraphic section of the Middle Triassic sediments in the Monte San Giorgio with distribution of the insect fossils (right). Stratigraphic log modified from Bechly & Stockar (2011).

San Giorgio includes terrestrial groups, with phytophagous and predatory habits, as well as aquatic groups, collected as larvae (e.g., Plecoptera) and as adults (e.g., Ephemeroptera). The diversity of the entomofauna from the Kalkschieferzone, together with the high biodiversity of the fish assemblage (Lombardo et al. 2012), supports the presence of a complex paleoenvironment in the area of Monte San Giorgio, which is known to have been a shallow lagoon, with limited connections to the open and deeper sea, adjacent to a carbonate platform, with permanent fresh water pools or small streams (Strada et al. 2014). Remarkably, so far no amphibian remains have been collected, although the paleoenvironment looks favourable for their life and they are quite common in the coeval rocks of the German Basin (Schoch 2006).

Among the insect fossil assemblage of Monte San Giorgio one specimen attributed to true bugs was discovered (Strada et al. 2014) and is

herein described and named.

Within true bugs, Cimicomorpha, with approximately 20.000 described species, represent the most diverse and successful lineage of Heteroptera. Representatives of this group possess heterogeneous ecology and have successfully colonized a broad variety of habitats, with the evolution of different habits spanning from predation to phytophagy, the former retained as the groundplan feature of Heteroptera (Cobben 1978; Schuh et al. 2009). On the basis of the fossil record, the first extant cimicomorphan families have made their appearance in the Jurassic, with the first occurrence represented by Nabidae (Cimicoidea) and Miridae (Miroidea) in the Jurassic (Carpenter 1992; Hou et al. 2012; Nicholson et al. 2015). Within Tingioidea, three extant families have been recognized by Lis (1999), namely the Vianaididae, Tingidae, and Cantacaderidae. Other authors (Froeschner 1996; Froeschner 2001; Golub 2001)

recognised only the two families of Vianaididae and Tingidae, the latter including Cantacaderinae as a subfamily together with Tinginae (Schuh et al. 2006). Members of Vianaididae and Tingidae have been recovered from the Cretaceous Period (Popov 1989; Golub & Popov 2000; Golub & Popov 2003a; Perrichot et al. 2006; Golub & Popov 2008). In addition to Vianaididae and Tingidae, three new fossil tingoid families have been recently described, namely Ignotingidae from the Laiyang Formation at the Jurassic-Cretaceous boundary (Zhang et al. 2005), Ebboidae from Albian amber of France (Perrichot et al. 2006) and Hispanocaderidae from Lower Cretaceous amber of Spain (Golub et al. 2012).

Within Tingidae, encompassing approximately 2100 extant species worldwide distributed (Froeschner 1996), more than 40 fossil species are known from Lower Cretaceous to the Upper Miocene (Golub 2001; Wappler 2003; Golub & Popov 2003a; Golub & Popov 2003b; Nel et al. 2004; Perrichot et al. 2006; Wappler 2006; Golub & Popov 2008; Heiss & Guilbert 2013; Wappler et al. 2015). Thus, currently the oldest lace bugs fossils are *Sinaldocader drakei* Popov, 1989 and *Sinaldocader ponomarenkoi* Golub & Popov, 2008 from the Lower Cretaceous of Eastern Siberia, and *Golmonia pater* Popov, 1989 from the Lower Cretaceous of Mongolia, all assigned to the subfamily Cantacaderinae. *Spinitingis ellenbergeri* Heiss & Guilbert, 2013 and *Tingiometra burmanica* Heiss et al., 2015 from Upper Cretaceous Burmese amber are the oldest known fossil belonging to the subfamily Tinginae.

Here we describe a new genus and species of lace bugs (Hemiptera: Tingidae), *Archetingis ladinica* gen. n., n. sp., which brings back the origin of Tingidae to Middle Triassic and has relevant evolutionary and ecological implications. The holotype, the only known specimen, is a compression fossil of ~12 mm preserved in ventral view.

MATERIAL AND METHODS

The specimen has been collected in locality D in Val Mara, near Meride (Canton Ticino, Switzerland) and will be deposited at Museo Cantonale di Storia Naturale di Lugano. Specimen manipulation and measures were completed with the auxiliary use of the stereomicroscope Zeiss Axio Zoom V16 with a digital camera Zeiss AxioCam 506. Images were acquired at different focus layers that were mounted with Zerene Stacker 1.0. The obtained images

were processed using Adobe Photoshop CS3. The drawing of the taxon has been produced using graphics tablet (Intuos®pro, Wacom) and Adobe Illustrator CC.

TAPHONOMIC REMARKS

The specimen here described, preserved in part and counterpart, has maintained the general layout of the body, including the three tagma, as well as most of the appendages. However, two out of the six legs and the two antennae, with the exception of the basal antennomeres, are displaced. This preservation suggests that the organism went through a first stage of decay in subaerial and/or superficial aquatic environment, during which part of appendages were disarticulated and lost. Therefore, we hypothesize that short after the death and a preliminary decay on terrestrial environment, the insect was transported by not high-energy events, such as a water run-off after monsoons (as previously suggested, see Tintori 1990a,b; Tintori & Brambilla 1991) or by wind, to the depositional basin where, after a fast sinking to the bottom, burial and fossilization took place. Since most of the specimen's body layout is preserved, we can hypothesize a time-limited decay, a short transportation, and a final depositional environment without bottom currents, in anoxic and possible hyperhaline conditions (Lombardo et al. 2012; Strada et al. 2014). No traces of phosphatization are present: this is consistent with what is recorded for the Coleoptera from the Kalkschieferzone, no one of them showing phosphatization. This latter preservation seems to be typical of other insect groups, such as the Archaeognatha (Montagna et al. 2017) or representative of other orders still under study.

SYSTEMATIC PALAEOLOGY

Order **Hemiptera** Linnaeus, 1758
 Suborder **Heteroptera** Latreille, 1810
 Infraorder **Cimicomorpha** Leston, Pendergrast
 & Southwood, 1954
 Superfamily **Tingoidea** Laporte 1833
 Family **Tingidae** Laporte, 1833
 Genus *Archetingis* gen. n.

Type species: *Archetingis ladinica* n. sp. by monotypy.

Code Zoobank: urn:lsid:zoobank.org:act:0850BA23-1C83-4A9D-99F2-690829F49413

Etymology: The name of the genus is combined from *archè-* (greek), which means origin, since we consider this taxon as the possible most recent common ancestor of the crown Tingidae, and *-tingis* from the name of the family (Tingidae Laporte, 1833) to which the specimen is assigned.

Diagnosis: Dimensions above family maximum length; macropterous. Head short with laterally protruding eyes, hypognathus with rostrum inserting on the ventral face; bucculae closed at the anterior end, not extending beyond apex of head; rostrum moderately long, extending at least to the base of metasternum; presence of labial groove on meso and metathoracic sternum. Extended areole on forewings (one/two rows of areole protruding beyond abdomen margin and tip) and on pronotum, carina not visible. Legs I and II with thick femurs and elongated tibiae; tarsi two-segmented, visible on leg II of the left side (fig. 2).

Archetingis ladinica n. sp.,
figs 2, 3.

Code Zoobank: urn:lsid:zoobank.org:act:02013C8E-0044-4238-B2AB-9C375E7BAA1F

Etymology: The name is derived from the age of the strata from which the specimen was collected, i.e., the Ladinian.

Type specimens: MCSN8459, holotype, the only known specimen.

Type horizon: Uppermost part of the Lower Kalkschieferzone (upper Member of the Meride limestone); Bed 18 of Site D, Val Mara (fig. 1).

Type locality: Specimens collected at site D, Val Mara near Meride (Mendrisio), Canton Ticino, Switzerland (fig. 1).

Repository: MCSN8459 specimen will be deposited at Museo Cantonale di Storia Naturale di Lugano - Switzerland.

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

Description. Large specimen of 11.8 mm preserved in ventral view both on slab and counterslab (fig. 2A, B), partially disarticulated with the right leg I detached and superimposed on left leg I. Almost all head appendages (except left antennomer I), right leg II, second pair of wings not preserved. Head, thorax, abdomen, five legs preserved. Pronotum and hemelytrae partially preserved. Body not elongated. Hemelytrae with one-two rows of cells extending beyond abdomen margins and tip of abdomen; cells of regular shape until the two-thirds of hemelytra, of growing dimensions towards the apex, smaller on pronotum (fig. 2A, B, F; fig. 3). Macropterous form.

Head partially preserved, large and short, 1.5 mm long, 1.8 mm wide (fig. 2 A, B; fig. 3A). Triangular frons, spines and tubercles absent; first antennomer preserved on the left; antennal tubercles visible. Eyes of medium size, globular, projecting laterally beyond head margins. Mouthparts forming a piercing/sucking rostrum; bucculae not reaching the apex of the head, closed anteriorly. Two segments of the rostrum preserved, possibly disarticulated, extend-

ing until metasternum (fig. 2A, C; fig. 3A).

Pronotum 5.7 mm long, 4.5 mm wide. Central portion partly visible through the ventral structures, areole small (fig. 2A, B; fig. 3A). Upper and lateral (left side on slab) rim preserved, areolate, one row of regularly shaped areole preserved, larger than on inner part. Scutellum and carinae not visible. External margin of hemelytra with areole, clearly visible on the right side of the abdomen on slab (fig. 2A), left side on counterslab (fig. 2B, F). Areole of increasing size towards apex of wings, areola on tip of hemelytra at the left side of the abdomen 0.64 mm wide. Hemelytra protruding from abdomen for approximately 0.5 mm. Ridges not visible.

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 on left leg II, 1.07 mm long. Tibiae of the forelimbs thickest; markedly widening at the distal end; tibia on left leg I 0.62 mm thick at the apex. Punctuations clearly visible on right femur I (fig. 2B, D; fig. 3A).

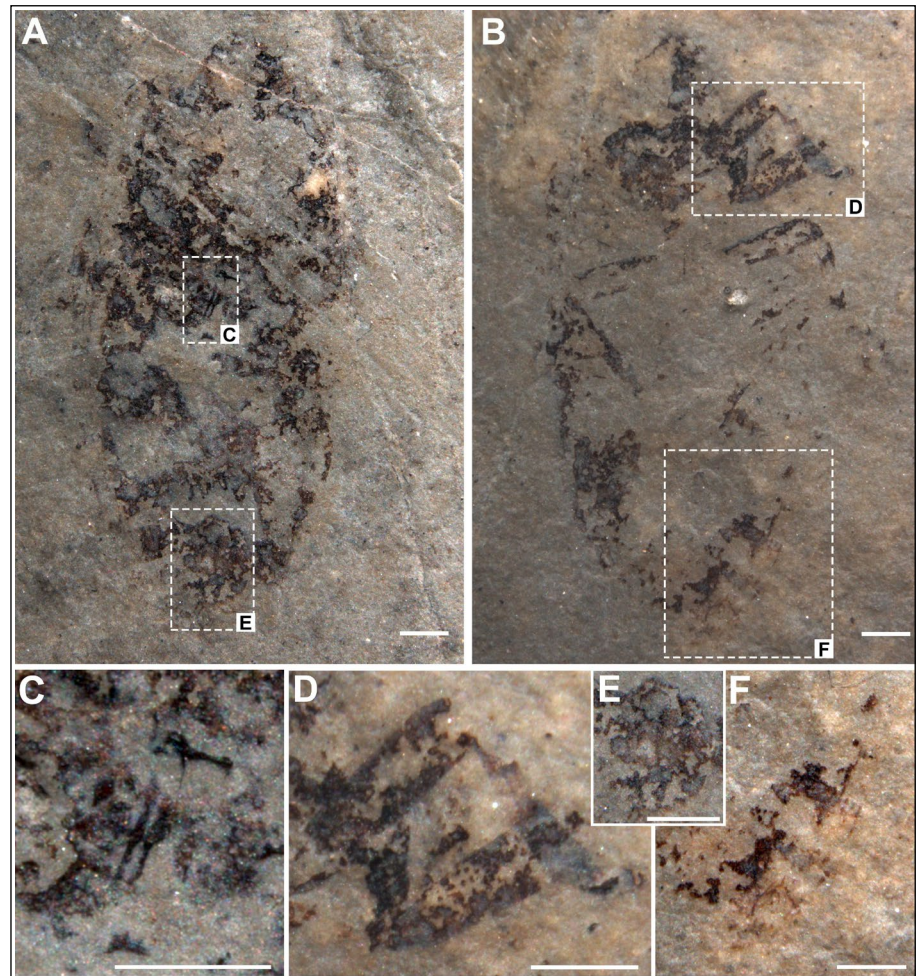
Abdomen length 6.1 mm, approximate width at base 4.5 mm. Male specimen, genital capsule visible (fig. 2A, B, E; fig. 3A), 1.74 mm large and 1.66 mm long.

DISCUSSION

Archetingis ladinica differs from all the known fossil specimens for its great dimensions and the very thick foretibiae. The phytophagous feeding behavior of *A. ladinica*, supposed also for all other fossil Tingidae and shared by most extant species, is confirmed by the bucculae closing before the end of the head, thus preventing the forward extension of the rostrum, necessary for predation. The general habitus of *A. ladinica* resembles that of the extant genera *Acalypta* Westwood, 1840, *Campylosteira* Fieber, 1844, *Dictyonota* Curtis, 1827, *Kalama* Puton, 1876 and *Tingis* Fabricius, 1803 (fig. 4); however, on the basis of the present data, no close phylogenetic relationships could be hypothesized between *A. ladinica* and the reported extant genera.

The discovery of *A. ladinica* in the Lower Kalkschieferzone of Monte San Giorgio brings back the origin of lace bugs of approximately 140

Fig. 2 - *Archetingis ladinica* n. sp., holotype (MCSN8459). A) slab; B) counterslab; C) magnification of the rostrum, from the slab; D) magnification of the fore femora (disarticulated) highlighting the strong punctuation, from left side of the counterslab; E) magnification of the genital capsule, from the slab; F) magnification of the areole on hemelytra, from the left side of the abdomen on the counterslab. On A and B images are reported, with dotted white boxes, the regions corresponding to images from C to F. White scale bars correspond to 1 mm.



My, from the Lower Cretaceous (*Sinaldocader drakei*, *Golmonia pater* and *Sinaldocader ponomarenko*) into the Middle Triassic. Moreover, the finding of *A. ladinica* from Middle Triassic and the recent description of three Tingoidae families close to lace bugs from the Jurassic-Cretaceous boundary (Ignotingidae Zhang, Golub, Popov & Shcherbakov, 2005) and from Lower Cretaceous (Ebboidae Perrichot, Nel, Guilbert & Neraudeau, 2006; Hispanocaderidae Golub, Popov & Arillo, 2012) supports Pericart's view that Tingidae were well established before the breakup of Pangea. It also suggests a high diversity of tingoid lineages during the Mesozoic, well before the radiation of flowering plants that occurred at the Lower Cretaceous (e.g., Friis et al. 2006; Magallón et al. 2015). The paucity of plant remains in the Lower Kalkschieferzone, including only few remains of the gymnosperm *Voltzia*-like and of horsetails (Furrer 1995; Felber 2005, A.T. pers. obs.), prevents us from providing a detailed reconstruction on *A. ladinica* host plants. The flora from a slightly older fossiliferous level of Monte San Giorgio, the Cassina Beds,

has been accurately reconstructed thanks to the collection of several plant remains and it is dominated by different genera of conifers as *Elatocladus*, *Voltzia* and *Pelourdea*, and by the seed ferns of the genus *Ptilozamites*, (Stockar & Kustatscher 2010). Based on the preserved morphological features, it seems that *A. ladinica* lacks of a rostrum adapted to pierce and suck on thick cuticle, as possessed by gymnosperms of the Ladinian of Monte San Giorgio (Stockar & Kustatscher 2010). Considering the wide spectrum of host plants and trophic behaviours possessed by the extant Tingoidae families, which include feeding on mosses and rootlets within the ant nests, the absence in *A. ladinica* of a robust rostrum leads us to hypothesize that horsetails, ferns or mosses with a thin cuticle could have represented its host plants.

The insect fossil assemblage of the Lower Kalkschieferzone (239.51 ± 0.15 Ma; Stockar et al. 2012) is nowadays composed of 19 specimens belonging to six different extant orders of insects, with both terrestrial and freshwater habits (Krzeminski & Lombardo 2001; Strada et al. 2014; Montagna et al.

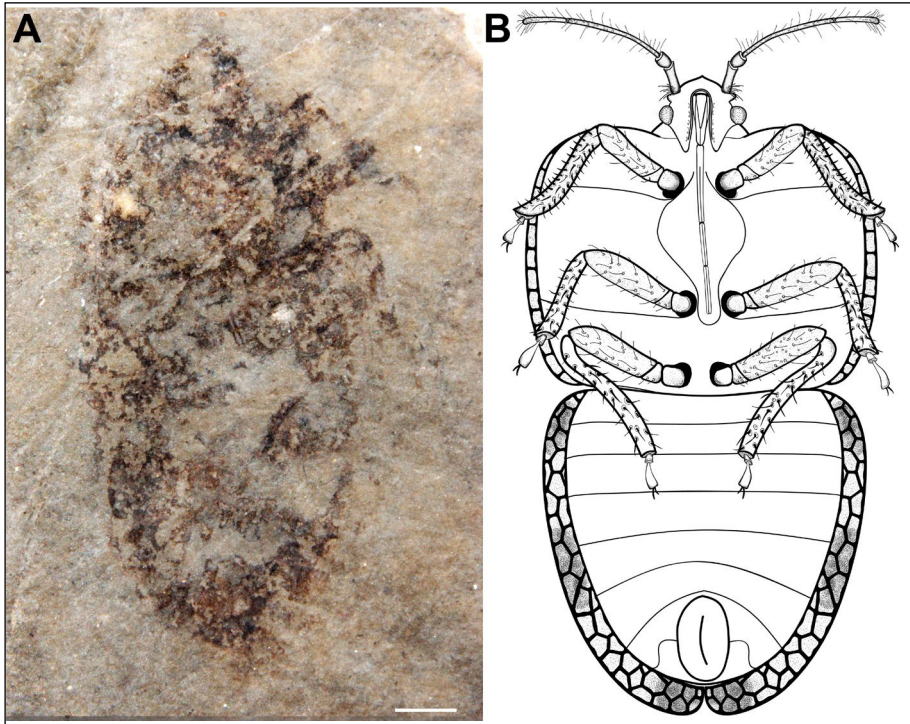


Fig 3 - A) *Archetingsis ladinica* n. sp., holotype (MCSN8459) obtained merging slab and counterslab; B) reconstruction of *Archetingsis ladinica* n. sp. (drawing made by Matteo Montagna), in grey are reported features not preserved in the fossil (i.e., antennae and eyes). The white scale bar corresponds to 1 mm.

2017). Six specimens have been assigned to terrestrial taxa as Trachypachidae and Cupedidae among Coleoptera, Embioptera, Orthoptera and, now, to Hemiptera; eight specimens, preserved at adult and larval stages, are members of Ephemeroptera, Plecoptera and Coleoptera (Coptoclavidae), which require permanent fresh water pools or small streams to complete their development. At present, four taxa have been formally described: the mayfly *Tintorina meridensis* (Krzeminski & Lombardo 2001), two beetles, *Praedodromeus sangiorgensis* (Strada et al. 2014)

and *Notocupes* sp. (Krzeminski & Lombardo 2001) and the bristletail *Gigamachilis triassicus* (Montagna et al. 2017). A further bristletail species, *Dasyleptus triassicus* (Bechly & Stockar 2011) has been described from the Upper Kalkschieferzone. Previous studies have described the paleoenvironment of the Kalkschieferzone as that of a shallow lagoon, adjacent to a carbonate platform, with nearby small islands and large emerged land (Tintori 1990a; Tintori & Lombardo 1999; Lombardo et al. 2012). The presence of terrestrial and freshwater ecosystems nearby

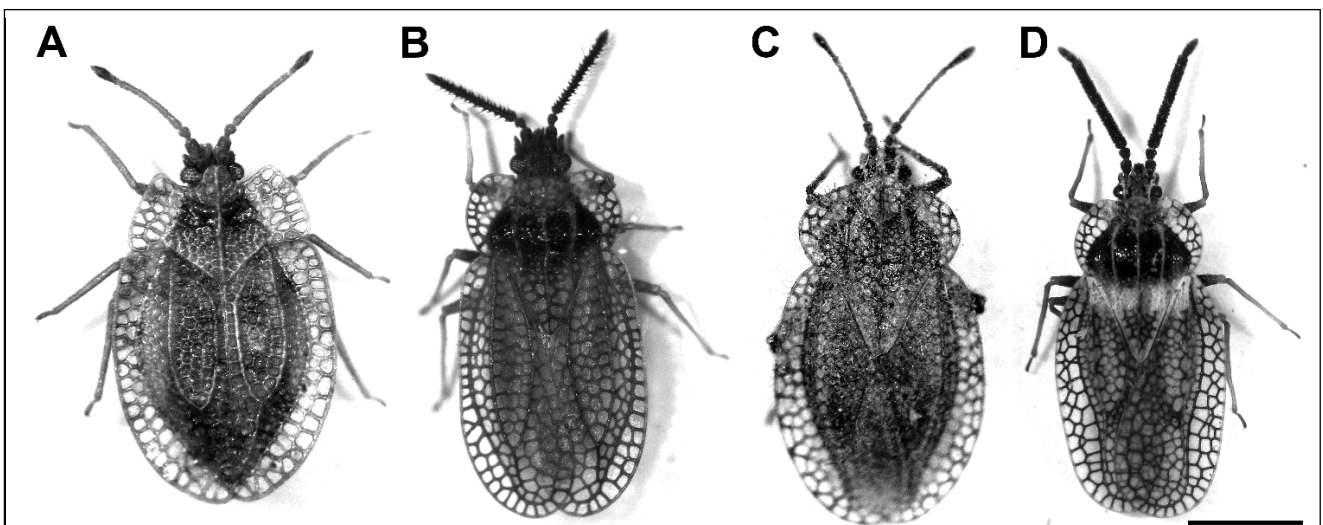


Fig 4 - Representatives of extant genera with a general habitus resembling that of *Archetingsis ladinica*. A) *Acalypta musci* (Schrank, 1781); B) *Kalama tricornis* (Schrank, 1801); C) *Tingis reticulata* Herrich-Schäffer, 1835; D) *Dictyonota strichnocera* Fieber, 1844. The scale bar corresponds to 1 mm.



Fig. 5 - Slab with remnant of the coniferous *Voltzia* (Voltziales) and some estherids of the genus *Palaeolimnadia* (Branchiopoda). The scale bar corresponds to 2 cm.

the depositional environment has already been supported by previous studies on arthropods (Tintori 1990a; Krzeminski & Lombardo 2001; Strada et al. 2014; Montagna et al. 2017). Assuming that the living environments and the ecology of *A. ladinica* could be inferred from that of extant lace bugs, we can hypothesize that *A. ladinica* inhabited terrestrial environments characterized by the presence of gymnosperms of the genus *Voltzia* (fig. 5) and other vascular plants such horsetails and ferns, but possibly also by the presence of bryophytes. The discovery of *A. ladinica* provides further evidence for the presence of complex environments able to support a diversified insect fauna in term of both taxa and of ecology.

Interestingly, the body-size of *A. ladinica* is larger than that of extant lace bugs, usually in the range between 1.5 and 6 mm, with the largest taxon so far known not reaching 1 cm (Pericart 1983); the same pattern has been also observed in the case of the giant bristletail *G. triassicus* (Montagna et al. 2017). The

presence in the Lower Kalkschieferzone of insects with a very large body-size, if compared with extant representatives, might be explained by the broad advantages in competition and defence possessed by gigantic organisms. Besides to the previously postulated effect of the changes in atmospheric temperatures on the evolution of taxa with large body-size (Montagna et al. 2017), a possible alternative explanation relies on the evolution of the competitively driven divergence of large and small body-size taxa on the small islands of the Lower Kalkschieferzone paleoenvironment.

The terrestrial environment surrounding the Lower Kalkschieferzone basins is apparently poor as so far only conchostracans estherids and rare coniferous *Voltzia* remains have been recorded (fig. 5). Conchostracans can be very common at least in horizons where fishes are almost lacking (Tintori 1990a) proving the presence of fresh water ponds to support the whole life-cycle of these short living crustaceans. However, insects from the Kalkschieferzone are rarely on the same surfaces yielding conchostracans. Furthermore, in the Monte San Giorgio, they are recorded mainly in the upper part of the Lower Kalkschieferzone, although conchostracans are very common also in the Middle Kalkschieferzone, as recorded for Ca' del Frate site (Tintori 1990a; Tintori & Brambilla 1991). At Ca' del Frate, preservation of arthropods is usually quite nice, with soft parts sometimes well visible such as in conchostracans were also eggs can be preserved (Tintori 1990a). Also, the common mysidacean *Schimperella*-like (Larghi & Tintori, submitted) can show phosphatization of soft parts. Thus, lacks of insects in the Middle Kalkschieferzone cannot be related to preservation or to collecting biases.

We want to underline also that the richest plant assemblage in the Ladinian from Monte San Giorgio is from the lower Meride Limestone Cassina Beds (Stockar & Kustatscher 2010). However, from that fossiliferous horizon no insects or fresh waters dwellers have been recorded. Thus, it seems that good condition (superficial fresh water, vegetation) for insects life on nearby emerged land was a common feature during the deposition on the Meride Limestone and quality of preservation was almost the same at least during the Kalkschieferzone deposition.

Why insect specimens have been recorded mostly at site Val Mara/Meride D at the top of the Lower Kalkschieferzone, remains without an answer.

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