

The first Mesozoic record of the extinct apterygote insect genus *Dasyleptus* (Insecta: Archaeognatha: Monura: Dasyleptidae) from the Triassic of Monte San Giorgio (Switzerland)

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Abstract

Dasyleptus triassicus n. sp. (Monura: Dasyleptidae) is described from the Ladinian (Middle Triassic) Meride Limestone of Monte San Giorgio in Switzerland. It is the first fossil record of an apterygote insect from the Triassic, and the first Mesozoic record of the extinct group Monura. Monurans were previously only known from the Palaeozoic Upper Carboniferous and Lower Permian. This new discovery shows that these delicate insects did survive the great end-Permian mass extinction event. *Dasyleptus* is considered to be a neotenic bristletail that lived at the drift line of sea shores and banks of freshwater bodies and swamps. A sister group relationship of Dasyleptidae with Ectognatha is rejected as insufficiently founded, and Monura is confirmed as a suborder of Archaeognatha, which represents the sister group of all Recent bristletails (suborder Machilida n. stat.). Fossil insects with unusual features, described from the Carboniferous of Mazon Creek as '*Dasyleptus*' spec. by KUKALOVÁ-PECK, are here considered as "chimeras" from three different organisms: 1) genuine monurans; 2) Cercopodata; 3) stem group insects unrelated to Dasyleptidae but maybe congeneric with the alleged fossil silverfish *Ramsdelpidion*. Their status as genuine fossil evidence is supported and claims of "intensive preparation" rejected as insufficiently founded.

Key words: fossil insects, Archaeognatha, Machilida, Monura, Dasyleptidae, *Dasyleptus*, *Triassomachilis*, Mesozoic, Middle Triassic, Ladinian, Meride Limestone, Monte San Giorgio, Switzerland.

Zusammenfassung

Dasyleptus triassicus n. sp. (Monura: Dasyleptidae) wird aus dem Ladinischen (Mitteltrias) Meride-Kalke von Monte San Giorgio in der Schweiz beschrieben. Es handelt sich um den ersten Fossilnachweis eines flügellosen Insektes in der Trias und um den ersten mesozoischen Nachweis der ausgestorbenen Gruppe Monura. Diese waren zuvor nur aus dem paläozoischen Oberkarbon und Unterperm bekannt. Die neue Entdeckung belegt, dass diese zarten Insekten das große Massenaussterbeereignis am Ende des Perm überlebt hatten. *Dasyleptus* wird als neotener Felsenpringer angesehen, der am Spülsaum von Meeresküsten und am Ufer von Süßgewässern und Sümpfen lebte. Ein Schwestergruppenverhältnis von Dasyleptidae und Ectognatha wird als unzureichend begründet zurückgewiesen und die Monura als Unterordnung der Archaeognatha bestätigt, die in einem Schwestergruppenverhältnis zu allen rezenten Felsenpringern (Unterordnung Machilida n. stat.) stehen. Fossile Insekten mit ungewöhnlichen Merkmalen, die aus dem Karbon von Mazon Creek als '*Dasyleptus*' spec. von KUKALOVÁ-PECK beschrieben wurden, werden hier als „Chimären“ aus drei unterschiedlichen Organismen erachtet: 1) echte Monuren; 2) Cercopodata; 3) Stammgruppenvertreter der Insekten, die nicht mit den Dasyleptidae verwandt sind, die aber vielleicht mit dem angeblichen fossilen Silberfisch *Ramsdelpidion* kongenerisch sind. Ihr Status als authentische Fossilien wird unterstützt und die Behauptung von „Überpräparation“ als unzureichend begründet zurückgewiesen.

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1. Introduction

The fossil apterygote insect genus *Dasyleptus* was described by BRONGNIART (1885) and was a typical faunal element of the Carboniferous and Permian sea shores and swamps. SHAROV (1957) erected a separate family Dasyleptidae and a new order Monura for these insects. Such a distinct status was also advocated by KUKALOVÁ-PECK (1987, 1991), who attributed strange fossil apterygote insects from Mazon Creek to '*Dasyleptus*' spec. within Monura, which was disputed by the majority of subsequent authors. HENNIG (1969) and WILLMANN (2003a, b) also considered Monura as distinct order and as the sister group of Ectognatha. TOJO & MACHIDA (2001) attributed *Dasyleptus* and Monura to the Ectognatha (incl. Archaeognatha, Zygentoma, and Pterygota), based on the synapomorphic presence of a caudal filament (terminal filum) as elongation of the telson (epiproct). BITSCH & NEL (1999) followed CARPENTER (1992) in downranking Monura to a suborder of the Recent order Archaeognatha. GRIMALDI (2001: 1153; 2010) also concurred with RASNITSYN (1980, 2000) that *Dasyleptus* is not belonging to a separate order Monura but is just a "large juvenile" [sic] of the extant order Archaeognatha. New species of *Dasyleptus* have been described by DURDEN (1978), RASNITSYN (2000), RASNITSYN et al. (2004), and ENGEL (2009). BITSCH & NEL (1999), RASNITSYN (2000), and ENGEL (2009) revised this group, and ENGEL (2009) also provided a determination key to all six known species. Several features of the morphology of *Dasyleptus* and their implications for the ground plan reconstruction of Hexapoda have been discussed by BITSCH (1994). A revised and amended diagnosis and phylogenetic analysis of Monura was provided by WILLMANN (2003a).

The palaeoecology of monurans was briefly discussed by MÁNGANO et al. (2001) and SINITSHEKOVÁ (2003). RINEHART et al. (2005), who studied the ontogenesis of *Dasyleptus brongniarti*, could identify six instars with a very similar growth pattern (following Prizibram's rule) as in Recent Archaeognatha and Zygentoma.

We here describe a new species of the genus *Dasyleptus* from three specimens from the Meride Limestone of Monte San Giorgio, as the first Triassic record of an apterygote insect and the first Mesozoic record of the suborder Monura and a surprising survivor of the end-Permian extinction event.

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and generous support during his visit in May 1996, and for an unpublished draft of the manuscript KUKALOVÁ-PECK & BEUTEL (in prep.). The second author is indebted to the many students and volunteers who helped during the excavation and to Prof. SILVIO RENESTO (Uninsubria, Varese) for having suggested the institutional collaboration which made this study possible. Dr. NERIA RÖMER (MCSN) provided assistance with the photographs of the type material. Financial support for the field work was granted by the Dipartimento del territorio del Cantone Ticino (Museo Cantonale di Storia Naturale, abbreviation MCSN) and the Swiss Federal Office for the Environment (FOEN).

2. Material and methods

The first specimen of the fossils described here (MCSN 8343, holotype) was discovered in August 2010 by the second author in the Upper Kalkschieferzone of the Upper Meride Limestone during the geological survey for his PhD work. In the following month of September, he led a detailed excavation of the Cantonal Museum of Natural History (MCSN), which yielded two further specimens coming from the same bed (MCSN 8344 and MCSN 8345, paratypes). These two further specimens were found by MARTINA RAVIOLI and SERGIO PEZZOLI.

The specimens have been mechanically prepared with a steel needle. The drawings have been made from macro photos of the fossils. All figures have been subsequently edited and polished with the Adobe Photoshop™ CS3 imaging software.

The specimens of fossil "apterygotes" from Mazon Creek mentioned and featured in this paper are all from the collection of JARMILA KUKALOVÁ-PECK (coll. JKP) at Carleton University in Ottawa (Canada). They have been studied and photographed by the first author during a research visit in 1996.

3. Geology, stratigraphy and taphonomy

The Middle Triassic succession at Monte San Giorgio (Fig. 1) starts with a fluvio-deltaic sequence dated to the late Anisian (Bellano Formation, Illyrian; SOMMARUGA et al. 1997), overlying a Permian volcanic succession. The upper Anisian sediments testify to the progressive transgression of a shallow epicontinental sea and the related growth of carbonate platforms (Lower Salvatore Dolomite; ZORN 1971) north of a land area buried today under the Po Plain (the Southern Mobile Belt of BRUSCA et al. 1981; PICOTTI et al. 2007). During the latest Anisian and Ladinian, whereas in the north shallow-water sedimentation continued, in the Monte San Giorgio area the formation of a 30–100 m deep and 10–20 km wide intraplatform basin with restricted circulation (FURRER 1995) resulted in the deposition of the Besano Formation, the San Giorgio Dolomite and the Meride Limestone.

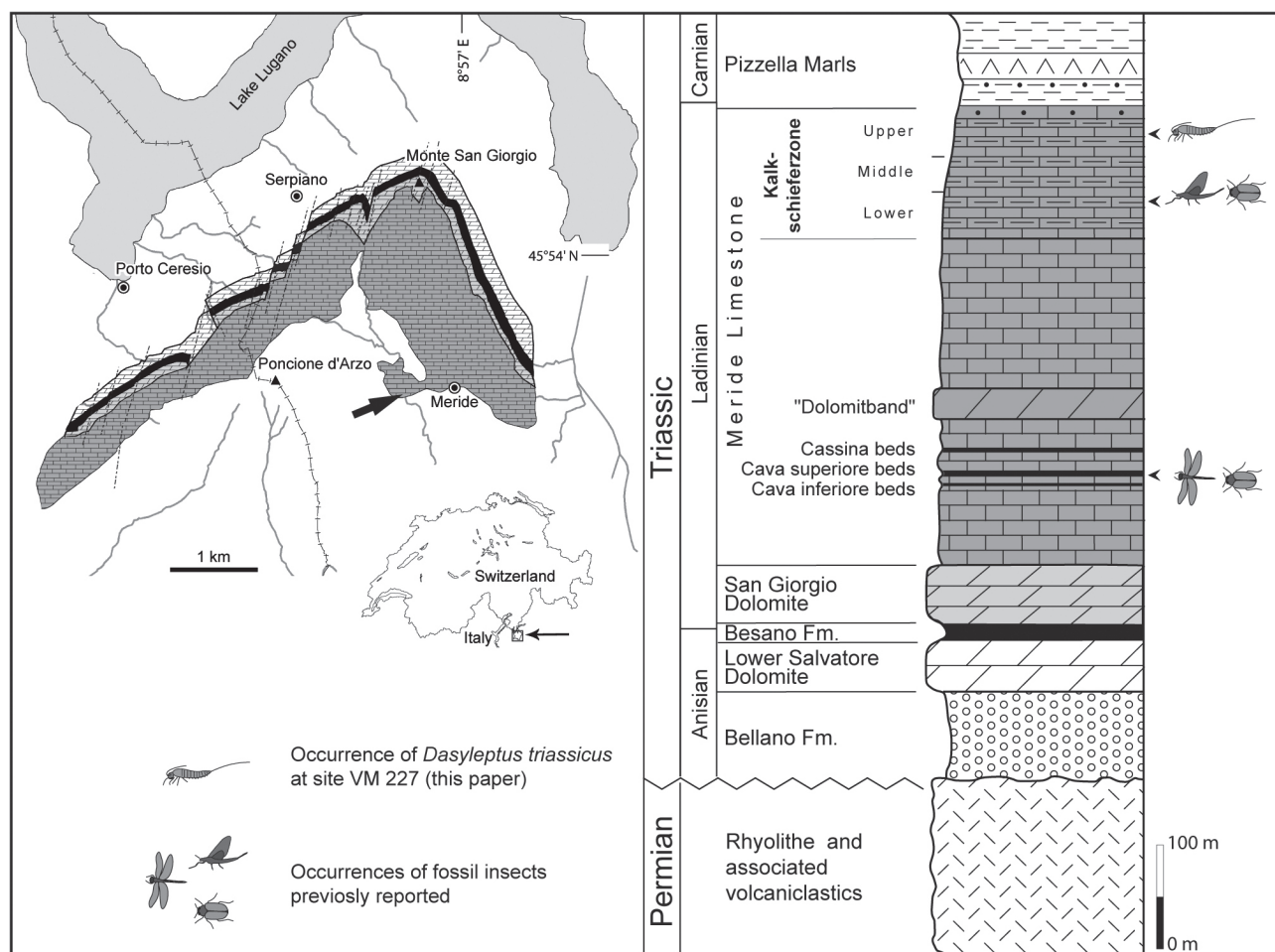


Fig. 1. Map of the Monte San Giorgio area (left) showing the Middle Triassic carbonate sequence and location (arrow) of the site VM 227 (from STOCKAR 2010) and stratigraphic distribution of the insect fossils from Monte San Giorgio (right). Stratigraphic log modified from FURRER (1995).

The Besano Formation (“Grenzbitumenzone”; FRAUENFELDER 1916), is an alternation of black shales and dolomites up to 16 m thick, including in its uppermost part the Anisian-Ladinian boundary (BRACK et al. 2005); a volcanic ash layer lying a few metres below this boundary resulted in an U-Pb minimum age of 242.1 ± 0.6 Ma (MUNDIL et al. 2010). The Besano Formation, which yielded most of the spectacular vertebrate fossils (reptiles and fishes) together with important index fossils such as ammonoids and daonellid bivalves, grades upwards into the 60 m thick San Giorgio Dolomite. The overlying 400–600 m thick Meride Limestone (FURRER 1995) begins with the Lower Meride Limestone, which bears three fossil tetrapod beds (Cava inferiore, Cava superiore and Cassina beds), each yielding different vertebrate assemblages (e. g. BÜRGIN 1999; SANDER 1989; STOCKAR 2010) and consisting of finely laminated limestones with intercalated volcanic ash layers.

The top of the Lower Meride Limestone is defined by a dolomite bed (“Dolomitband”; FRAUENFELDER 1916). The overlying Upper Meride Limestone is a sequence of alternating well-bedded limestones and marlstones with an increasing clay content towards the top. The uppermost part is the 120 m thick “Kalkschieferzone”, the unit which yielded the fossils described in the present paper, and which has been dated by SCHEURING (1978) to the late Ladinian on the basis of its palynological content. WIRZ (1945) divided the Kalkschieferzone into three subunits (Va, Vb and Vc), afterwards called Lower, Middle and Upper Kalkschieferzone by FURRER (1995). The Kalkschieferzone is mainly made up of thin-bedded limestones and marlstones with volcanic ash layers and bears peculiar reptile and fish faunas, terrestrial plants and crustaceans, the latter including conchostracans. The habitat of living and fossil conchostracans rules out normal marine conditions and includes temporary inland ponds, flood-plain

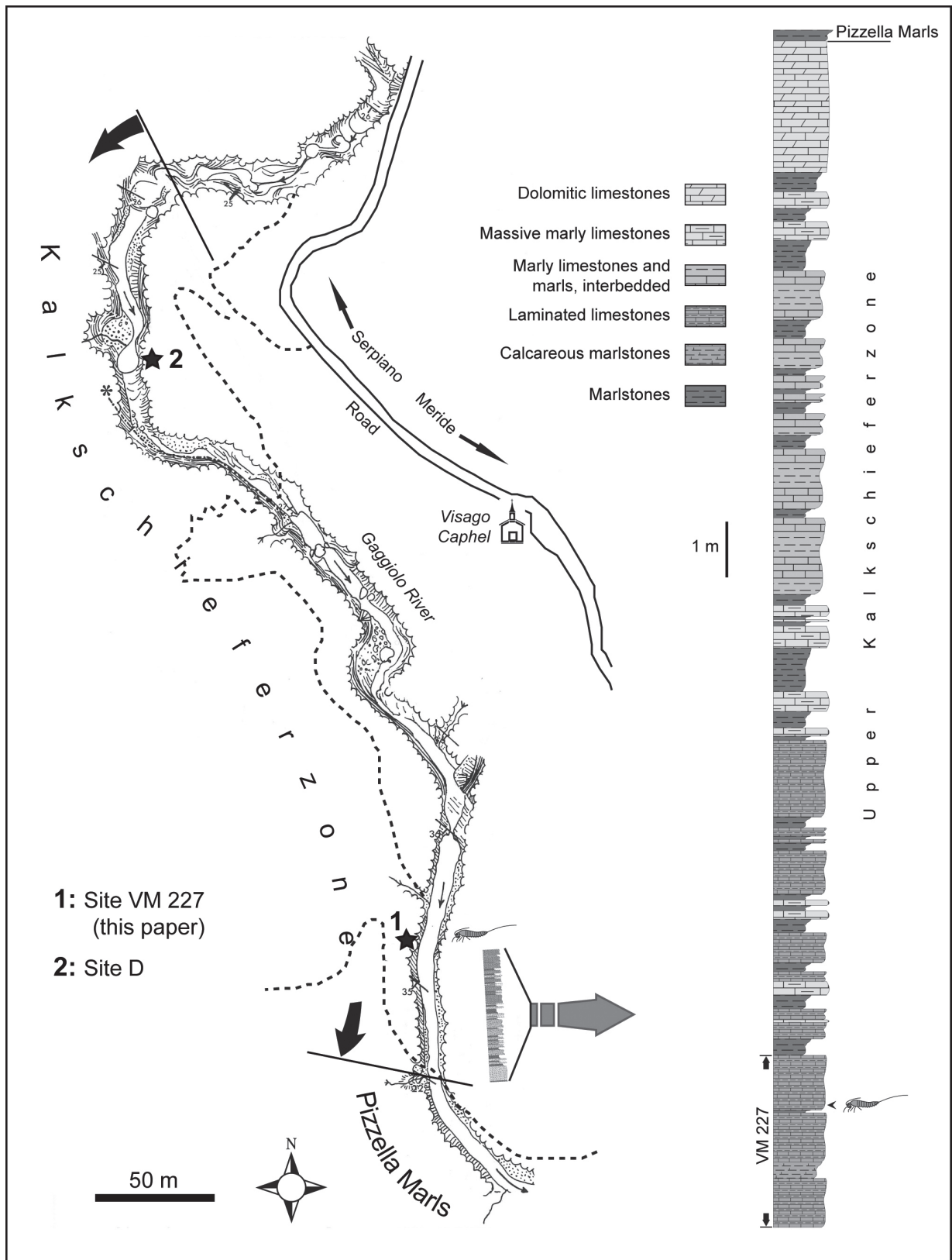


Fig. 2. Map of the Gaggiolo valley (“Val Mara”. After SCHEURING 1978, modified) and stratigraphic section of the uppermost Kalkschieferzone.

pools, coastal flood-plains and brackish water estuarine and deltaic environments (KOZUR & WEEMS 2010).

The peculiar depositional environment of the Kalkschieferzone is regarded as a shallow lagoon recording strong seasonal variations of salinity and water level. During Ladinian times, the depositional environment was located within the subtropical zone at a palaeolatitude of around 18°N (BRACK et al. 1999) and was influenced by a monsoonal climate (MUTTI & WEISSERT 1995). The resulting sedimentation is likely the product of alternating dry seasons, with low water level and high salinity, and wet seasons during which the hypersaline lagoon was flooded by lighter freshwater, resulting in density stratification with brackish surface water and oxygen-depleted bottom water (FURRER 1995). TINTORI (1990) regarded the dense concentrations of conchostracans occurring in the Kalkschieferzone as allochthonous populations transported during the rainy season into the marine or brackish basin. This scenario was disputed by FURRER (1995) who considered the concentrations of conchostracan crustaceans as autochthonous populations developed during extraordinary rainy seasons in the shallow areas of the basin, flooded by fresh water, and subsequently killed during the dry season by the increasing salinity and decreasing oxygenation.

In the latest Ladinian an increasing input of siliciclastic material was probably related to the erosion of the Southern Mobile Belt and more in general to the following Carnian regressive phase. It resulted in the formation of sabkha-type depositional environments and in the related sedimentation of evaporites (Pizzella Marls; FURRER 1995). According to SCHEURING (1978) the Ladinian/Carnian boundary lies above the base of the Pizzella Marls.

The bed yielding the specimens described here belongs to the Upper Kalkschieferzone where a small excavation on a surface of around two square meters was carried out in 2010 by the Cantonal Museum of Natural History (MCSN) under the direction of the second author. The site is located in the valley of the Gaggiolo River, also known as “Val Mara”, west of Meride village (Swiss National Coordinates: 717°090/83°170; Fig. 2). The investigated section (VM 227) consists of an 2.6 m thick alternation of thin-bedded laminated limestones and marly limestones with subordinated marlstones and calcareous marlstones. It lies somewhat below the layer 108 of SCHEURING (1978) and around 20 m below the base of the Pizzella Marls, which contains the Ladinian / Carnian boundary (SCHEURING 1978). The common absence of bioturbation points to anoxic conditions at the water/sediment interface. All the specimens studied here come from a single bedding plane of a grey thin-bedded laminated limestone bed, immediately overlying a 5 cm thick marlstone bed. Diffuse small land plant remains are the only other fossil occurrences from this bed together with five complete

small actinopterygian fish specimens, which are ascribed to *Peltopterus* sp. (two specimens) and to *Prohalecites porroi* (three specimens). Terrestrial plant remains occur throughout the Middle Triassic carbonate sequence at Monte San Giorgio, testifying to the presence of emerged areas (terrestrial areas or islands) covered with vegetation from which plant fragments could have been blown during rainy or storm events into the basin (STOCKAR & KUSTATSCHER 2010). *Peltopterus* is a small basal actinopterygian fish widely represented throughout the Monte San Giorgio section, with a surprising intra- and interspecific variability (LOMBARDO 1999). *Prohalecites porroi* is a small neopterygian fish widespread throughout the Kalkschieferzone where it sometimes constitutes mass mortality layers; according to FURRER (1995), the mass mortality events occurred during the dry season, being triggered by the strong evaporation increasing the salinity. However, our *Prohalecites* specimens do not testify to such mass mortality events, their frequency on bedding planes being too low and their skulls being never bent backward (FURRER 1995).

As a whole, the above features suggest that the deposition occurred during the rainy season. This is consistent with a transport by overflows into the basin of the insect remains described here, regarded as belonging to coastal dwellers (see further below). In addition, water mass stratification occurring during the wet season tends to confine circulation to the surface water and to favour the offshore transport of buoyant terrestrial components (TYSON 1995; STOCKAR & KUSTATSCHER 2010).

4. The fossil entomofauna from Monte San Giorgio: state of the art

The first discovery of insect fossils from Monte San Giorgio dates back to 1998. It consists of three specimens from the so-called “Site D” of the Lower Kalkschieferzone (Fig. 2), which have been ascribed to *Tintorina meridensis* (Ephemeroptera. MCSN 4666, MCSN 5001) and to *Notocupes* sp. (Coleoptera. MCSN 5002) (KRZEMINSKI & LOMBARDO 2001). Two further fossil insects were collected in 1999 from Cava Superiore beds (Lower Meride Limestone) during excavations carried out by the Palaeontological Institute and Museum of the University of Zurich (PIMUZ) in collaboration with the Cantonal Museum of Natural History (MCSN). These findings, a dragonfly and a beetle whose study is currently in progress, are stored at the MCSN (catalogue numbers MCSN 4994 and MCSN 4995). Further material, collected between 2000 and 2003 at “Site D” (see above) during excavations carried out by the University of Milan (UNIMI) in collaboration with the MCSN, belongs to the MCSN collection and is currently under study at UNIMI.

5. Systematic palaeontology

Order Archaeognatha BÖRNER, 1904

Suborder Monura SHAROV, 1957

(= Mononemura CRAMPTON, 1916; = Archentomata
BOUDREAUX, 1979)

Family Dasyleptidae SHAROV, 1957

Genus *Dasyleptus* BRONGNIART, 1885

(= *Lepidodasypus* DURDEN, 1978)

Typus generis: *Dasyleptus lucasi* BRONGNIART, 1885. The spelling "*Dasyleptus Lukasii* Brgt." by BRAUER (1886: 88) has to be considered as an incorrect subsequent spelling according to IRZN.

Other species: *D. brongniarti* SHAROV, 1957, *D. sharovi* (DURDEN, 1978) (originally described in a separate genus *Lepidodasypus*), *D. artinskianus* ENGEL, 2009, *D. noli* RASNITSYN, 2000, *D. rowlandi* RASNITSYN et al., 2004, and *D. triassicus* n. sp. Furthermore, the three species of the ichnofossil

Tonganoxichnus MÁNGANO et al., 1997 have been interpreted as traces from jumping monuran hexapods (GUERRA-SOMMER et al. 1984; MÁNGANO et al. 1997, 2001; BRADY & BRIGGS 2002), but this was doubted by RASNITSYN (2000). A second unnamed species of *Dasyleptus* from Carrizo Arroyo was described by RASNITSYN et al. (2004), but this attribution is doubtful in our view since 14 body segments are visible and the habitus rather looks like a myriapod than a monuran.

Dasyleptus triassicus n. sp.

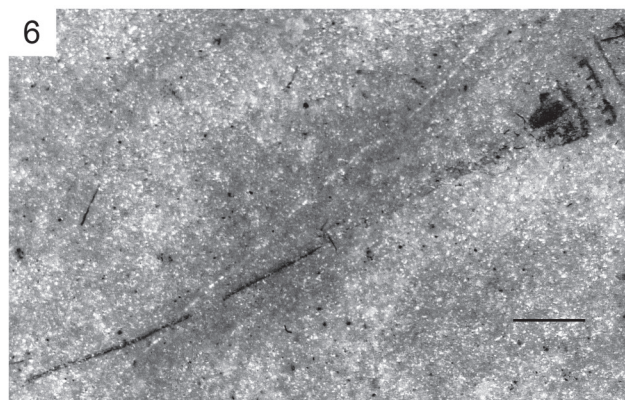
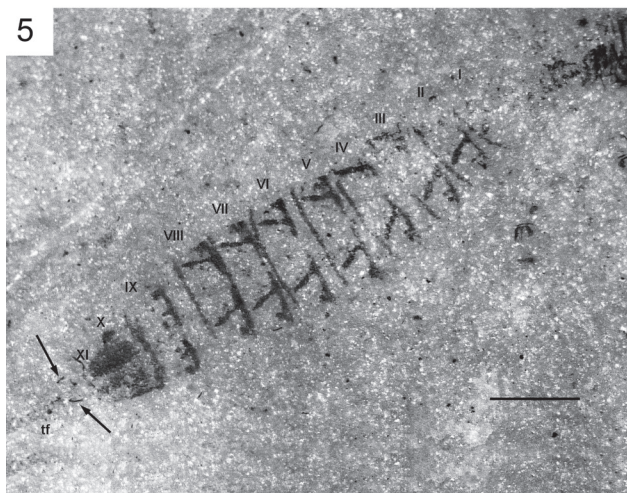
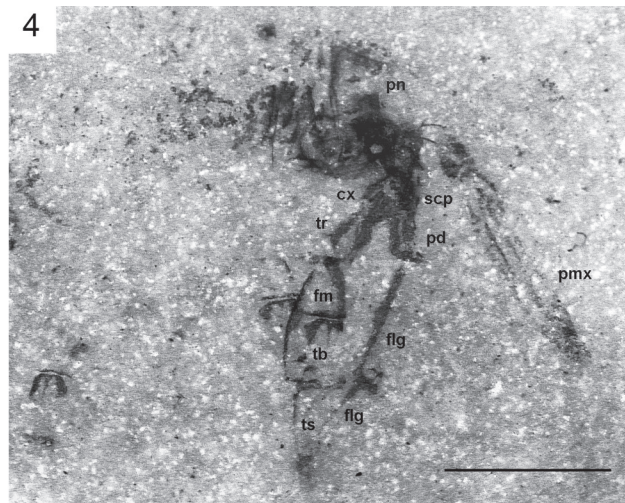
Figs. 3–13

Holotype: MCSN 8343 (Figs. 3–6), deposited at the Cantonal Museum of Natural History in Lugano (Switzerland).

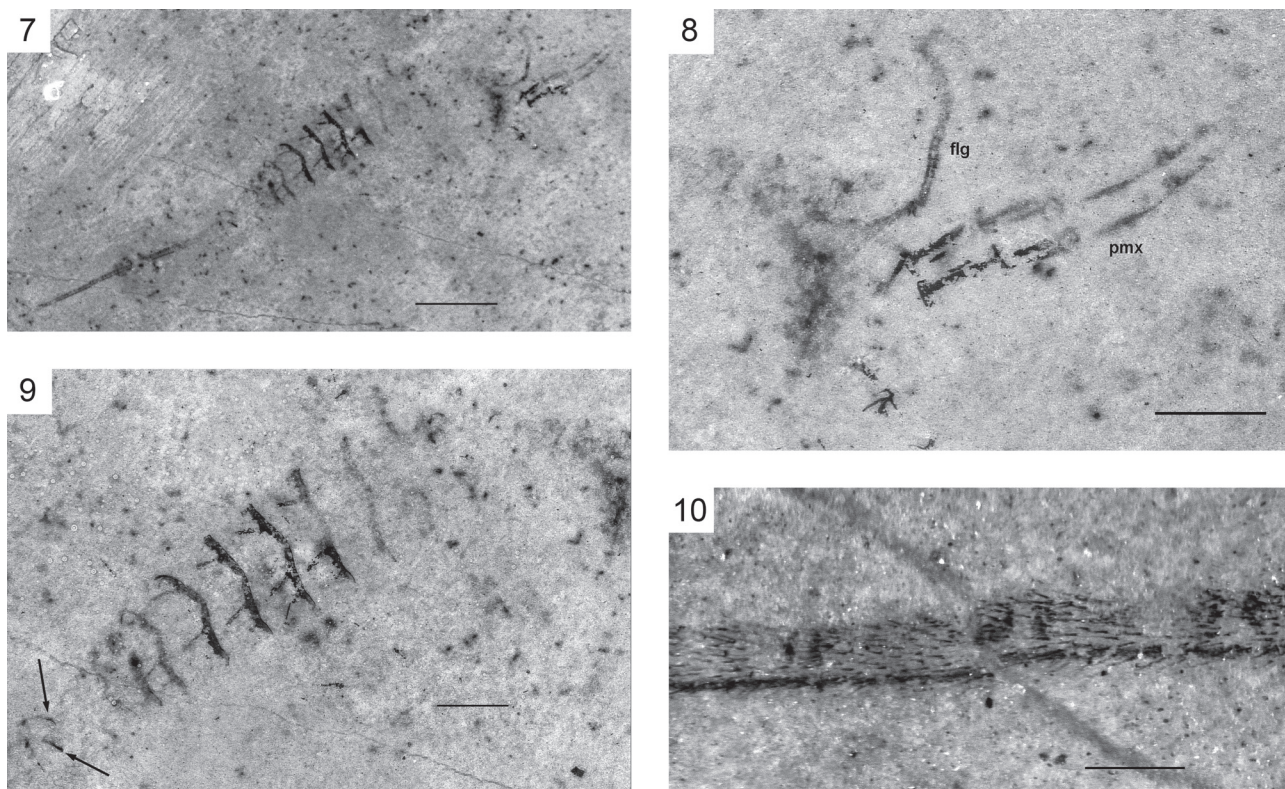
Paratypes: Specimens nos. MCSN 8344 (Figs. 7–10) and MCSN 8345 (Figs. 11–13).

Derivatio nominis: Named after the Triassic period.

Stratum typicum: Middle Triassic, Late Ladinian, Upper Kalkschieferzone (uppermost part of the Meride Limestone section, around 236 mya).



Figs. 3–6. *Dasyleptus triassicus* n. sp., holotype; MCSN 8343. – **Fig. 3.** Body. **Fig. 4.** Head, pn = pronotum, pmx = palpus maxillaris, scp = scapus, pd = pedicellus, flg = flagellum, cx = coxa, tr = trochanter, fm = femur, tb = tibia, ts = tarsus. **Fig. 5.** Abdomen, tf = terminal filum, arrows indicate potential vestiges of cerci. **Fig. 6.** Terminal filum. – Scales: Fig. 3: 2.0 mm, Figs. 4–6: 1.0 mm.



Figs. 7–10. *Dasyleptus triassicus* n. sp., paratype; MCSN 8344. – **Fig. 7.** Body. **Fig. 8.** Head, flg = flagellum, pmx = palpus maxillaris. **Fig. 9.** Abdomen, arrows indicate potential vestiges of cerci. **Fig. 10.** Detail of terminal filum. – Scales: Fig. 7: 2.5 mm, Figs. 8–9: 1.0 mm, Fig. 10: 0.2 mm.

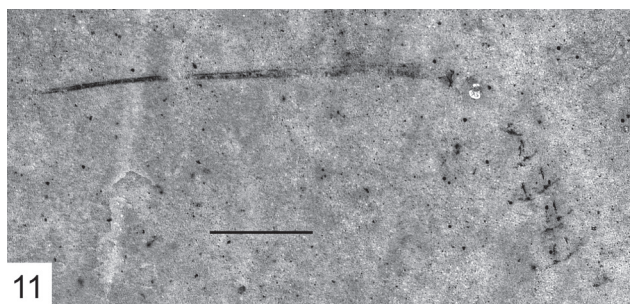
Locus typicus: Triassic Unesco Site Monte San Giorgio, Canton Ticino, Switzerland.

Diagnosis. – This new species shares the main characters of the Palaeozoic representatives of the genus *Dasyleptus*, such as large maxillary palps, short antennae, abdominal styli, and a long terminal filament but no visible cerci. It mainly differs from all other species of *Dasyleptus* in the very broad legs, the number and structure of abdominal styli (?), and in the much younger Middle Triassic age (instead of Upper Carboniferous or Lower Permian). It differs from *Dasyleptus brongniarti* in the antenna that is longer than the head, it differs from *Dasyleptus noli* in the not widened largest segment of the maxillary palp, and it differs from *Dasyleptus rowlandi* in the terminal filum that is longer than the abdomen. Furthermore, it differs from *Triassomachilis* SHAROV, 1948, meanwhile considered to be a mayfly nymph of the genus *Mesoneta*, in the absence of paired cercal filaments, the presence of abdominal styli, a much more elongate body, and much larger maxillary palps.

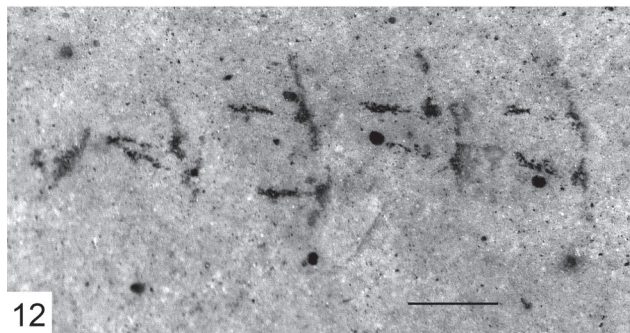
Description of holotype (Figs. 3–6). – A complete insect in ventral view; head and thorax seem to be somewhat smashed; thoracic terga saddle-shaped; legs detached and only one leg is well preserved, with

very short and broad segments (max. width 0.34 mm at tibia), maybe even flattened; only one maxillary palp is partly preserved, which can be identified as maxillary palp instead of leg because of an elongate segment that is 1.35 mm long and 0.22 mm wide; the antenna has a very thick scapus (0.25 mm long, 0.21 mm wide) and pedicellus (0.27 mm long, 0.15 mm wide), and a short flagellum (1.2 mm long); total body length 15.5 mm; abdomen with 11 segments, length of abdomen ca. 5.7 mm, max. width 1.3 mm; a pair of unsegmented and non-annulated styli (0.34–0.39 mm long) without apical spine is visible on the venter of abdominal segments 2–8, but inconspicuous or absent on segments 9–10, maybe also missing on the first segment that is not clearly visible; terminal filum completely preserved and 7.7 mm long (longer than abdomen) and 0.17 mm broad at base; cerci absent or vestigial (see discussion); no genital organs visible.

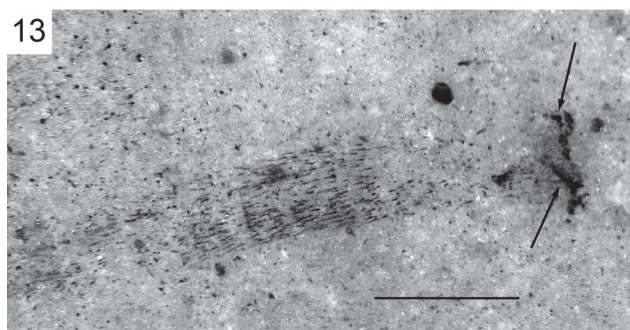
Description of paratypes (Figs. 7–13). – Specimen MCSN 8344 (Figs. 7–10) is a complete animal in ventral view; two maxillary palps are anteriorly directed, 3.23 mm long, and at least six elongate segments are visible; short antenna, annulated flagellum 1.92 mm long (longer than head); body arched near thorax, 9.4 mm long (excl. appendages) and max. 1.85 mm wide; a pair



11



12



13

Figs. 11–13. *Dasyleptus triassicus* n. sp., paratype; MCSN 8345. – **Fig. 11.** Body. **Fig. 12.** Abdomen. **Fig. 13.** Base of terminal filum, arrows indicate potential vestiges of cerci. – Scales: Fig. 11: 2.0 mm, Figs. 12–13: 0.5 mm.

of unsegmented and non-annulated styli (0.33–0.42 mm long) without apical spine is visible on the venter of at least five abdominal segments; preserved length of terminal filum 6.1 mm (apex apparently missing), width 0.31 mm at base and 0.12 mm in middle part; terminal filum annulated and hairy; cerci absent or vestigial (see discussion); no genital organs visible.

Specimen MCSN 8345 (Figs. 11–13) is represented by an abdomen fragment with terminal filum; preserved length of abdomen (segments 6–10) about 4.3 mm; a pair of unsegmented and non-annulated styli (0.33–0.42 mm long) without apical spine is visible on the venter of segments 6–8, while segments 9 and 10 seem to lack styli; length of terminal filum 8.0 mm (probably longer than abdomen), width at base 0.28 mm; the terminal filum is

annulated and covered with hairs; cerci absent or vestigial (see discussion); no genital organs visible.

Remark. – In all three type specimens there are two tiny stylus-like structures visible at the base of the terminal filum, which may either be artefacts or rather vestiges of the cerci.

6. Discussion

6.1. Phylogenetic position of *Dasyleptus* and the status of Monura

Among apterygote insects the presence of abdominal styli (instead of leglets) could be a synapomorphy with Cercophora (Diplura + Ectognatha), because the abdominal styli of *Dasyleptus* (Figs. 5, 9, and 12) strongly differ from the larger segmented abdominal legs with paired claws in a putative stem group insect (Fig. 18) that has been incorrectly attributed to Monura (see discussion below on '*Dasyleptus*' sensu KUKALOVÁ-PECK).

The presence of an antennal flagellum and of a terminal filum are synapomorphies with Ectognatha, of which the terminal filum is only retained in Archaeognatha, Zygentoma, and Ephemera. The presence of a female ovipositor in *Dasyleptus brongniarti* could be a further synapomorphy with Ectognatha, but an ovipositor might indeed also be present (Fig. 18) in the above mentioned stem group insect from Mazon Creek (contra WILLMANN 2003b), so that the ovipositor could rather be a symplesiomorphy that is secondarily absent in Diplura, Protura, and Collembola.

HENNIG (1969: 109), KRISTENSEN (1975), BOUDREAUX (1979), and WILLMANN (2003a: 19–20; 2003b) proposed that Monura is the sister group of Ectognatha. For this hypothesis WILLMANN (2003a) listed the following five synapomorphies of Archaeognatha + Dicondylia that seem to be present in the plesiomorphic state in Monura: 1) styli absent on first abdominal segment; 2) subsegmented tarsi; 3) pretarsus with paired claws; 4) long ovipositor valves; abdominal segment 11 mostly reduced and fused with terminal filum. To this list we could add the prolonged flagellum of the antennae, which is still short in Monura, but long in Archaeognatha, Zygentoma, fossil stem group mayflies (Protoreisma), and many other basal pterygotes incl. Palaeodictyoptera, Plecoptera, Dictyoptera, Orthoptera etc.

However, it must be noted, that most of these characters could be better explained as paedomorphic reversals in *Dasyleptus* rather than as plesiomorphies, because they also occur in the late embryos of Archaeognatha (RASNITSYN 2000), such as short antennae, unsegmented tarsi, single claw, and suppressed cerci. Even the well-developed abdominal segment 11 could represent such a paedomorphic trait, because this segment is developed

in many insect embryos. The fact that paired claws are known from Diplura and from the above mentioned stem group insect (Fig. 18) supports the interpretation of a paedomorphic reversal in *Dasyleptus*. According to RASNITSYN (2000) all fossil monurans probably represent only juvenile stages but no adult specimens, which could also explain the short ovipositor valves as ontogenetic feature rather than as plesiomorphy. The only remaining character for a position of Monura as sister group of Ectognatha, which could not be explained with paedomorphosis, is the presence of styli on the first abdominal segment. Its absence in Recent Archaeognatha and Zygentoma rather seems to be due to convergence, because it is only a reduction and by convergence also reduced in Diplura. Furthermore, styli are clearly present on the first abdominal segment in *Ditrigoniophthalmus oreophilus* (KOCH 2003; clearly visible in the holotype according to KLUGE, pers. com. 2011), the Recent sister species of the remaining Machiloidea (KOCH 2003).

The alternative attribution of the *Dasyleptus* to the Recent order Archaeognatha was suggested by numerous authors (TIEGS & MANTON 1958; CARPENTER 1977, 1992; RASNITSYN 1980; CARPENTER & BURNHAM 1985; JARZEMBOWSKI 1987; and BITSCH & NEL 1999) and can be based on three putative synapomorphies: 1) enlarged maxillary palps; 2) cerci not more than half as long as epiproct or even completely reduced; 3) feeding cone for sucking mode of food uptake formed by narrow, elongate mouthparts (KOCH 2003). KOCH (2003) suggested two further putative synapomorphies: monocondylic mandibles and loss of cercal mobility. However, the interpretation of monocondylic mandibles as derived state is based on very dubious fossil evidence (see below), and the complete reduction of cerci in *Dasyleptus* does not allow the conclusion that reduced cercal mobility is a synapomorphy of *Dasyleptus* with Archaeognatha, rather than only an autapomorphy of Recent Archaeognatha. Nevertheless, the enlarged maxillary palps are a unique synapomorphy with Archaeognatha that has to be weighted much higher than conflicting reductive characters (especially if homoplastic), or a set of characters that can be explained by paedomorphosis. Also the arched posture and putative jumping behaviour (documented by trace fossils) suggest an archaeognathan affinity, even though the thorax is not bulged as in Recent Archaeognatha as adaptation to jumping (KOCH 2003). The latter character, as well as the unfused compound eyes, represent putative plesiomorphies that suggest a sister group relationship with Recent Archaeognatha (KOCH 2003), even though a paedomorphic reversal cannot be excluded.

Consequently, we concur with RASNITSYN (2002) and consider Dasyleptidae as a juvenilized extinct group of Archaeognatha, which should be classified in a suborder Monura. We propose to use the name Machilida for

a Recent suborder (sister group of Monura) that accommodates a new family for the most basal Recent species *Ditrigoniophthalmus oreophilus* and its sister group, the Recent superfamily Machiloidea (“Machilidae” + Meintertellidae).

6.2. Number and structure of abdominal styli in *Dasyleptus*

The well-preserved abdominal styli in all three type specimens are remarkable, because they are the best evidence currently available for this important character in Monura. The unsegmented and non-annulated abdominal styli without apical spine might seem to be a difference to the two- to four-segmented styli that had originally been described for monurans. However, according to the redescription of BITSCH & NEL (1999: 21) there are no visible styli in any of the 45 specimens of the type series of the type species *Dasyleptus lucasi*. One of these specimens was chosen by RASNITSYN (2000) as the holotype of *Dasyleptus noli* and also has no visible styli at all. Two-segmented styli on segment 1–9 had been described for *Dasyleptus brongniarti* by SHAROV (1957), but according to the redescription by RASNITSYN (2000) this species has annulated styli on segments 1–6 or 1–7 (visible on the stylus of the first segment in the holotype and paratype PIN 966/19, while the other 5–6 styli are poorly preserved and rather look unsegmented). *Dasyleptus sharovi* has annulated styli on segments 1–7 according to the original description by DURDEN (1978). The drawing by DURDEN shows a strange ovipositor that seems to be formed by valves of segments 7 and 8, which is anatomically impossible, because in all insects the ovipositor is formed by valves of segments 8 and 9 (also visible in *Dasyleptus brongniarti*). RASNITSYN (2000) reexamined and figured the holotype, which shows no traces of any styli and ovipositor or the other unusual features described by DURDEN (1978) such as scale-like hairs. Styli were not described by ENGEL (2009) for *Dasyleptus artinskianus*, but on the photo (ENGEL 2009, fig. 1) there are styli clearly visible on segments 1 and 2 (maybe also on segments 3 and 5), which are unsegmented and maybe annulated. Recent apterygote insect always have unsegmented abdominal styli without annulation (Diplura on segment 2–7, Archaeognatha on segments 1–9 in the most basal species *Ditrigoniophthalmus oreophilus* and on segments 2–9 in all other Machiloidea, and Zygentoma at most on segments 2–9, commonly on segments 2–7 or reduced). In pterygote insects unsegmented abdominal gills, which might be homologous to styli, are developed on segments 1–7 in Recent mayflies and on segment 1–9 in Permian stem group mayfly larvae (Protereismatidae). However, the obvious serial homology of abdominal styli and gonostyli in Recent

Archaeognatha and Zygentoma, combined with the presence of a pair of abdominal gills together with gonostyli on segment 9 in Permian mayfly larvae, seem to contradict a possible homology of mayfly gills with abdominal styli (KLUGE 2004). Alleged annulated abdominal styli in fossil ectognathous insects have been described as exites by KUKALOVÁ-PECK (1987, 1991, 1997 and many other of her publications), but are highly disputed (BETHOUX & BRIGGS 2008) and have not been confirmed by any other independent studies. RASNITSYN (2000: 152) discussed the problem of the abdominal styli in Dasyleptidae and concluded that they are three- to four-segmented on abdominal segments 1–6, and more elongate on segment 7 and 8, while their existence on segment 9 is doubtful. We can confirm their absence on segment 9 in the new species and consider the isolated cases of apparent segmentation as artifactual pseudo-annulation due to postmortal shrinking of these hardly sclerotized structures.

6.3. Palaeoecology of *Dasyleptus*

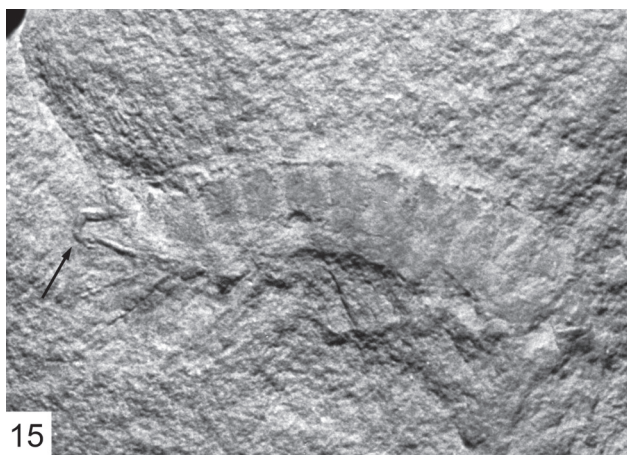
SINITSHENKOVA (2003: 382) presumed that Dasyleptidae probably had an aquatic or semi-aquatic way of life. However, this author acknowledged that Dasyleptidae do not exhibit any morphological aquatic adaptations, so that the case only rests on the common presence in the fossil record that is unique among apterygote insects. RASNITSYN et al. (2004) also stated that the available data imply a (sub) aquatic way of life for monurans. Indeed, alone the type series of *Dasyleptus lucasi* includes 45 specimens from the Commenry basin (BITSCH & NEL 1999), which has been a tropical swamp in the Carboniferous. Furthermore, 10 specimens of *Dasyleptus rowlandi* are mentioned by RASNITSYN et al. (2004) from the late Carboniferous palaeolake of Carrizo Arroyo (ROWLAND 1997), and RINEHART et al. (2005) studied 25 specimens of *Dasyleptus brongniarti* from Siberia. Also the Archaeognatha-like ichnofossils from Carboniferous estuary deposits in Kansas and Indiana (MÁGNANO et al. 1997, 2001; BRADY & BRIGGS 2002) and Permian deposits of Brazil (GUERRA-SOMMER et al. 1984) have been convincingly attributed to jumping monurans and suggest a way of life at the marine and brackish drift line and possibly also freshwater shores. Such a way of life is also known from some Recent archaeognathans like *Dilta littoralis*, *Petrobius brevistylis*, and *Petrobius maritimus*, who are however neither aquatic nor semi-aquatic. Since an adaptation to supralittoral habitats would greatly increase the likelihood of fossilisation we propose that Monura were not aquatic, but terrestrial coast dwellers at marine estuaries and the banks of freshwater bodies and swamps. As in the case of all 10 specimens of *Dasyleptus rowlandi*, most fossil monuran remains probably represent molting casts rather than the actual animals.

6.4. '*Dasyleptus*' sensu KUKALOVÁ-PECK

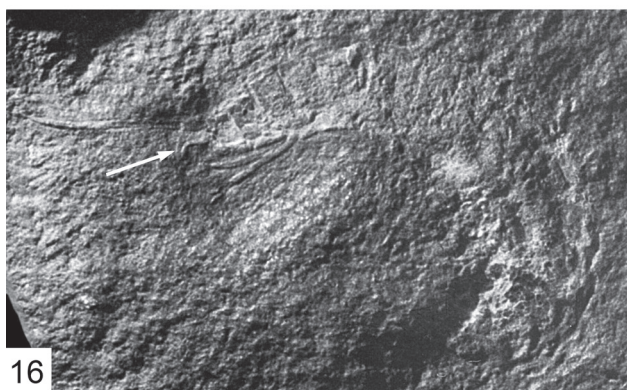
KUKALOVÁ-PECK (1987, 1991, 1997) and SHEAR & KUKALOVÁ-PECK (1990) maintained that Carboniferous and Permian archaeognathans have been confused with true monurans, and provided a reconstruction drawing of a "*Dasyleptus* spec. (Cercopodata: Monura)" from the Upper Carboniferous of Mazon Creek (Illinois, USA), which featured several unusual character states, such as six-segmented head with dicondylous mandibles, and abdominal and cercal leglets with paired claws. Even though this reconstruction of Monura strongly conflicted with the original descriptions of the true *Dasyleptus* species, it was uncritically accepted by AX (1999), HAAS et al. (2003), REGIER et al. (2004), and even used by HASENFUSS (2008) for a hypothetical scenario of insect wing evolution. However, KUKALOVÁ-PECK's description was doubted or even strongly disputed by BITSCH (1994), BITSCH & NEL (1999), RASNITSYN (2000, 2002), GRIMALDI (2001), WILLMANN (2003b), and BETHOUX & BRIGGS (2008). The latter authors even suspected "intensive" (to be understood as "creative" or "fraudulent") preparation. KUKALOVÁ-PECK & BEUTEL (in prep.) reject this accusation with the following argument: BETHOUX & BRIGGS (2008) maintained that "Tiny grains of pyrite are largely concealed within the matrix" and "Pyrite grains stand out in relief in areas of intense preparation, reflecting their resistance compared with the softer matrix", so that in combination with needle scratches and depigmentation they constitute positive proof that a thick layer of matrix above the fossil insects was removed and the insect surface heavily prepared and artificially sculptured. KUKALOVÁ-PECK & BEUTEL (in prep.)



Fig. 14. *Dasyleptus* sp. from Mazon Creek, specimen without no. in coll. JKP. – Without scale.



15



16



17

Fig. 15–17. Cercopodata from Mazon Creek, three specimens without no. in coll. JKP; arrows indicate segmented cercal leglet with paired claws. – Without scale.

present evidence that the pyrite aggregates are much softer than the ironstone nodules and that those micro-crystals of pyrite often grow directly on the fossils with the sulfur for micro-crystals being supplied by the decaying bodies. This would be clearly corroborated by BAIRD et al. (1986), who stated that “This pyrite typically occurs as spherical halos within sideritic concretions, usually surrounding

or occurring just above fossil nuclei”. Consequently, such pyrite structures would indeed rather suggest that no “heavy preparation” was applied, because that would have removed this coating on the surface of the fossil.

The first author had the opportunity to examine some of the original material of Mazon Creek apterygotes during a visit at KUKALOVÁ-PECK’s laboratory, as well as photos and casts of the crucial fossil specimens. There is no doubt that the described structures are well visible in the concerning fossils (Figs. 14–18; also see WILLMANN 2003b, figs. 1–4), and even though some interpretations by KUKALOVÁ-PECK may well turn out to be over-enthusiastic and guided by preconceived evolutionary scenarios, we consider claims of fabrications by intensive preparation as unfounded or at least not demonstrated beyond reasonable doubt. However, there is indeed no evidence that all the fossils in question are related to monuran Dasyleptidae, and it rather looks like that three different types of fossil apterygote insects from Mazon Creek have been used by KUKALOVÁ-PECK to produce a chimeral reconstruction, as was already presumed by WILLMANN (2003b): A) true monurans of the genus *Dasyleptus* (Fig. 14, also see WILLMANN 2003b, Fig. 2); B) genuine Cercopodata (Figs. 15–17); C) an unnamed stem group insect with abdominal legs (Fig. 18). The attribution of the latter fossil to the stem group of insects was already proposed by WILLMANN (2003b), and we concur with BITSCH & NEL (1999) that it may be congeneric with the alleged silverfish *Ramsdelepidon* KUKALOVÁ-PECK, 1987, which was only described in a figure legend with a reconstruction drawing based on four specimens. However, we disagree with BITSCH & NEL (1999) to use the name Cercopodata KUKALOVÁ-PECK, 1987 (= Cercopoda KUKALOVÁ-PECK, 1997) for the stem group insect with abdominal legs, because the specimens from



Fig. 18. Stem group insect (cf. *Ramsdelepidion*?) from Mazon Creek, specimen without no. in coll. JKP; arrow indicates segmented abdominal leglets with paired claws. – Scale: 10 mm.

Mazon Creek on which the taxon Cercopodata was based, do not have large abdominal legs (Figs. 15–17). We rather consider Cercopodata as a group distinct from Monura and distinct from the *Ramsdelepidion*, and as putative sister group of Cercophora (Diplura + Monura + Ectognatha).

6.5. Permo-Triassic mass extinction

This new species of Dasyleptidae is the first fossil record for Archaeognatha in the Triassic, and the first Mesozoic record of the extinct suborder Monura, which was previously only known from the Upper Carboniferous of Commeny and Montceau-les-Mines (France) (300–295 mya) and the Lower Permian of Elmo (Kansas, USA) and Kuznetsk Basin (Russia) (260–258 mya) (TASCH 1973; CARPENTER, 1977; BURNHAM, 1994; BITSCH & NEL 1999; ENGEL 2009; the paper by CARPENTER & RICHARDSON 1985 “Archaeognatha (Insecta) from the Upper Carboniferous of Illinois” that was cited by CARPENTER & BURNHAM 1985 and others as “Psyche in press” apparently was never published). The new species extends the range of the suborder Monura for 22 million years into the Late Ladinian and close to the Ladinian/Carnian boundary (around 236 mya, MUNDIL et al. 2010), and proves that these delicate insects survived the single most pervasive extinction event for life GRIMALDI & ENGEL (2005: 70). The end-Permian extinction event (EPE), dating back to 252.4 mya \pm 0.3 (MUNDIL et al. 2004, 2010), was most probably caused by volcanism (Siberian Traps flood basalts) and maybe additional impact (WHITE & SAUNDERS 2005), lasted for about one million years, and extinguished 96% of all marine species and 70% of all terrestrial vertebrate species (BENTON 2003; SAHNEY & BENTON 2008; ERWIN 2008). The unexpected survival of monurans is interesting, because the end-Permian event was the only known mass extinction of insects and triggered the radiation of modern insects (LABANDEIRA & SEPKOSKI 1993). BETHOUX et al. (2005) and SHCHERBAKOV (2008a) confirmed that there was an important renewal of the entomofauna at the Permian-Triassic boundary, and LABANDEIRA & EBLE (2002) wrote the following about the major impact of the Permo-Triassic extinction event on the insect fauna:

“In the several Late Triassic deposits that are well-documented, known taxa consist overwhelmingly of lineages belonging to extant orders ..., and there is minimal carryover from Late Paleozoic lineages. Some family-level lineages of orders whose diversity is centered in the Paleozoic survived the end-Permian event into the earlier Mesozoic, such as the “Protorthoptera” ..., Miomoptera ..., and Glosselytrodea ..., but most typically Paleozoic clades are not recorded in post-Permian deposits (LABANDEIRA 1994), including monurans, paleodictyopteroids, protodonates, protelytropterans, caloneurodeans, and hypoperlids ...

with the exception of the Geraridae ... These data demonstrate that the end-Permian event was the single most important event affecting insect diversity, separating the Paleozoic Insect Fauna from the Modern Insect Fauna at the highest taxonomic levels.”

However, recently a palaeodictyopteran has been discovered from the Triassic of Kyrgyzstan (BETHOUX et al. 2010), and another insect group that survived the Permo-Triassic boundary are the damselfly-like odonates of the “protozygopteran” grade (NEL et al. submitted). DAVIS et al. (2010) showed that “many hexapod groups originated earlier and withstood extinction events better than previously realized”. SHCHERBAKOV (2008b) showed that aquatic insects were less affected by the Permian-Triassic crisis, and BETHOUX et al. (2010) suggested that “a number of Palaeozoic insect groups might have migrated to higher latitudes, where humid conditions prevailed during the Permian-Triassic aridisation of the palaeo-equatorial belt”. Recent evidence from Permian-Triassic land-plant diversity in South China suggests that there indeed have been refugial areas that were not that much affected by the end-Permian extinction event (XIONG & WANG 2011).

6.6. Note on the relationship of *Triassomachilis*

Triassomachilis uralensis was described by SHAROV (1948) from the Triassic of south Ural in a separate family Triassomachilidae within Archaeognatha. However, the preserved characters do not allow an attribution to Archaeognatha, especially since the main apomorphies of Archaeognatha (viz fused compound eyes, long maxillary palps, and short cerci) are all absent or not preserved. BITSCH (1994) still accepted it as close relative of Recent machilids, but BITSCH & NEL (1999) already supposed that it could be rather a mayfly nymph. SINITSHENKOVA (2000) redescribed the type material and synonymized *Triassomachilis* with the fossil mayfly genus *Mesoneta* BRAUER, REDTENBACHER & GANGLBAUER, 1889. According to this redescription the annulated abdominal styli that were figured in the original description, and which would contradict a mayfly affinity, are actually not visible in the two type specimens. The identification as mayfly nymph was confirmed by RASNITSYN (2002) and KLUGE (2004), who attributed Mesonetidae to Ephemeroptera incertae sedis.

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