Austrian Journal of Earth Sciences | Volume 101 | 52 - 59 | Vienna | 2008

The Pannonian Insect Fauna of Styria: A Preliminary Overview

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KEYWORDS

Styrian Basin
Biodiversity
Pannonian
Miocene
Insecta

Abstract

Well-preserved insects are reported in pelitic sediments from the Feldbach and Paldau Formation (Late Miocene: Early Pannonian) of the Styrian Basin, Austria. Herein we provide a brief overview of the hitherto recovered fauna. The fauna includes representatives of five insect orders, representing at least 10 morphospecies of the families Phrygaenidae (Trichoptera), Tipulidae (Diptera), putative Rhagionidae (Diptera), Carabidae and Chrysomelidae (Coleoptera), Formicidae (Hymenoptera), and a giant primitive termite near Termopsidae (Isoptera). The various identifiable morphospecies recovered to date are summarized.

Vorliegende Arbeit dokumentiert die bis dato bekannten fossilen Insektenreste aus pelitischen Sedimenten der Feldbach- und Paldau-Formation (Steirisches Becken, Spätes Miozän: Frühes Pannonium). Die Fauna umfasst Vertreter von fünf Insektenordnungen mit zumindest 10 Morphospezies der Familien Phrygaenidae (Trichoptera), der Tipulidae (Diptera), vermutlich der Rhagionidae (Diptera), der Carabidae, der Chrysomelidae (Coleoptera) und der Formicidae (Hymenoptera) sowie eine primitve, den Termopsiden nahestehende Riesentermite (Isoptera). Alle bisher entdeckten, bestimmbaren Morphospezies werden beschrieben.

1. Introduction

Knowledge of Late Miocene insect faunas from the Pannonian Basin is rather poor and few publications concern themselves with the scattered remnants of what is known today, and has been since at least the Late Paleozoic (Grimaldi and Engel, 2005), the most diverse group of life on earth. For example, Abel (1933) briefly reported about the discovery of a termite nest at Guntramsdorf (Lower Austria, Vienna Basin). Several insect taxa have been recovered and described from the Middle Pannonian locality Brunn-Vösendorf (Lower Austria, Vienna Basin) among various plant fossils, including ground beetles (*Carabus*), ichneumon wasps (*Exetastes*), chinch bugs (*Lygaeidae*), ants (*Aphaenogaster, Camponotus*), dark-winged fungus gnats (*Lycoria*), carrion beetles (Silphidae), dragonflies (*Aeshna*), and traces of mayflies (Polymitarcyidae) (Berger, 1950; Papp and Mandl, 1951; Papp and Thenius, 1954; Bachmayer, 1960, 1961; Thenius 1979; see also Ponomarenko and Schultz, 1988; Thenius, 1988). Some ant and beetle fossils of Middle and Late Pannonian age were described by Schlüter (1979) from northwestern Romania (Delureni, Chiuzbaia).

Conversely, from Pannonian deposits of the Styrian Basin only four, brief accounts of insects have been presented up to now. Initially, Gross (1998a) mentioned the finding of a beetle elytron and figured afterwards two additional insect remains from an outcrop at Paldau (Gross, 2000). Subsequently, Gross (2004a) recorded a well-preserved beetle elytron from the clay pit Mataschen near Kapfenstein and more recently Engel and Gross (2008) presented a giant termite wing from Paldau.

The finding of a dragonfly naiad at the site “Andritz, brickyard Wolf” in the area of the city of Graz (Knoll, 1902; Bachmayer, 1952) was formerly thought to be of Early Pannonian age (Winkler-Hermaden, 1957) but later turned out to be of late Middle Miocene (Sarmatian) age (Gross et al., 2007). Further Neogene insect discoveries in the province of Styria originated from Middle Miocene strata of Parschlug and Münzenberg near Leoben (e.g., Heer, 1847, 1849; Handlirsch, 1907; Beier, 1952; Nel, 1994; Nel et al., 1999; for geological summaries see Gruber and Sachsenhofer, 2001; Sachsenhofer et al., 2001).

Herein we provide a brief overview of the Pannonian insect fauna as revealed by current excavations in the Styrian Basin. A more thorough systematic treatment of particular taxa recovered will be detailed elsewhere (Engel and Gross, in press, in prep.). All material is deposited in the Landesmuseum Joanneum (LMJ), Graz.

2. Geological Setting and Paleoecology

Up to now three Pannonian localities in the Styrian Basin have revealed fossil insects: Mataschen, Paldau, and Münzengraben near Paldau (Fig. 1). These sites are located in the Eastern Styrian Basin, which is the westernmost part of the Pannonian Basin system. At the beginning of the Late Miocene the so-called Lake Pannon developed within the Pannonian Basin and existed for several millions of years (Kazmer, 1990; Magyar et al., 1999; Harzhauser and Mandic, 2008). Repeated lake-level oscillations led to a complex interplay of limnic, deltaic, and fluvial sedimentary environments, especially in proximal areas like the Styrian Basin. However, endemic mollusc lineages (e.g., of dreissenid bivalves), migration events of mammals (e.g., the equid *Hippotherium*), as well as seismic and paleomagnetic investigations permitted the establishment of a high-resolution stratigraphical framework, which can be

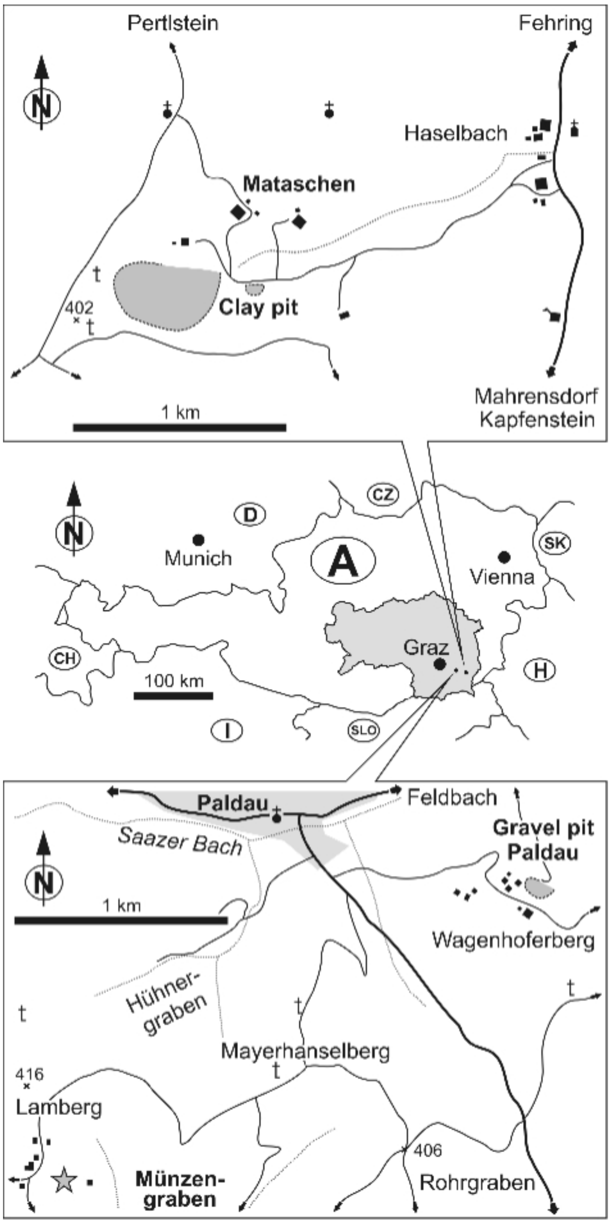

Figure 1: Geographic setting of insect-bearing Pannonian localities in the Styrian Neogene Basin (Mataschen, 46°54'15''N, 15°57'16''E; Paldau 46°56'17''N, 15°48'37''E, Münzengraben 46°55'39''N, 15°47'09''E).

used for intra- and extrabasinal correlations as well (e.g., Gross, 2004b; Schreilechner et al., 2007; Fig. 2).

2.1 Clay pit Mataschen (Early Pannonian, *Mytilopsis ornithopsis* Zone, c. 11.5 Ma)

The c. 30 m thick section of the clay pit Mataschen exposes a transgressive-regressive sedimentary cycle just above the Middle/Late Miocene boundary (Gross, 2004c; Fig. 2c). Whereas the lowermost sandy–silty layers were deposited in fluvial to marginal limnic environments, autochthonous tree stumps and coaly layers indicate up section the lakeside growth of a taxodiacean-swamp in an almost subtropical, largely frost-free climate. The herein described two beetle elytra and single caddisfly wing were found c. 0.5 m above these coaly layers in pelitic, bivalve- and leaf remain-bearing pelites. These strata were deposited in a shallow, freshwater to lightly saline lake shortly after drowning of the swamp.

The overlying pelites, with their rich micro- and macrofossil assemblages, document a rapid transgression and the establishment of basinal limnic conditions with up to polyhaline salinities (maximum flooding event). Pronounced terrigenous influx in the hanging wall marks the switch from lake-level rise to lake-level fall and a deltaic system started to prograde.

2.2 Gravel pit Paldau (Early Pannonian, *Mytilopsis hoernesi* Zone, c. 11.3 Ma)

In continuation of the aforementioned lake-level drop, fluvial systems developed in the area of Paldau (Gross, 1998a, b, 2003: Fig. 2b, c). This gravel pit provides insight into a typical fluvial fining-upward cycle of a meandering river with its various subenvironments. Aside from the specimens from Mataschen and the elytron from Münzengraben (see below), all hitherto known insect remains originate from a plant-rich, pelite layer close to the top of this outcrop. Sedimentological and paleobotanical analyses indicate an eutrophic, reed and riparian forest bordered floodplain pond as the sedimentary setting for this insect-bearing bed. Krenn (1998) proposed a warm temperate climate, close to subtropical, based on the fossil leaf-flora.

2.3 Outcrop Münzengraben near Paldau (Early Pannonian, *Mytilopsis hoernesi* Zone, c. 11.2 Ma)

After this fluvial phase, a short-term ingression of Lake Pannon is recognized at least in the eastern part of the Eastern Styrian Basin (Gross, 1998b, 2003; Kosi et al., 2003: Fig. 2b). However, pelitic, occasionally coal-bearing deposits of limnic-deltaic origin, led over to the following fluvial phase. In the outcrop at the westerly ditch of Münzengraben (Fig. 2c) a single elytron of a putative leaf beetle was found in limnic-deltaic pelites a few meters below fluvial gravels. The associated macroflora points to a nearby swamp and/or fen vegetation on a delta plain, which differs considerably from the riparian vegetation of the fluvial deposits (Gross, 1998a).

3. Systematic Paleontology

Order ISOPTERA Brullé, 1832

Among the more remarkable finds from the Late Miocene of Styria is that of a giant termite (Fig. 3a) (Engel and Gross, 2008, in press). The specimen is the forewing of a reproductive (an alate) and is complete with the forewing scale at its base indicating that it was not shed naturally from the insect as all winged termites do eventually after dispersal. The venation of the wing is very generalized and indicative of a grade of primitive termites between the Mastotermitidae, Termopsidae (*sensu* Engel et al., in press), Hodotermitidae (*sensu* Engel et al., in press), and modern relatives such as *Archotermopsis*, *Anacathotermes*, and *Hodotermopsis*. This grade is

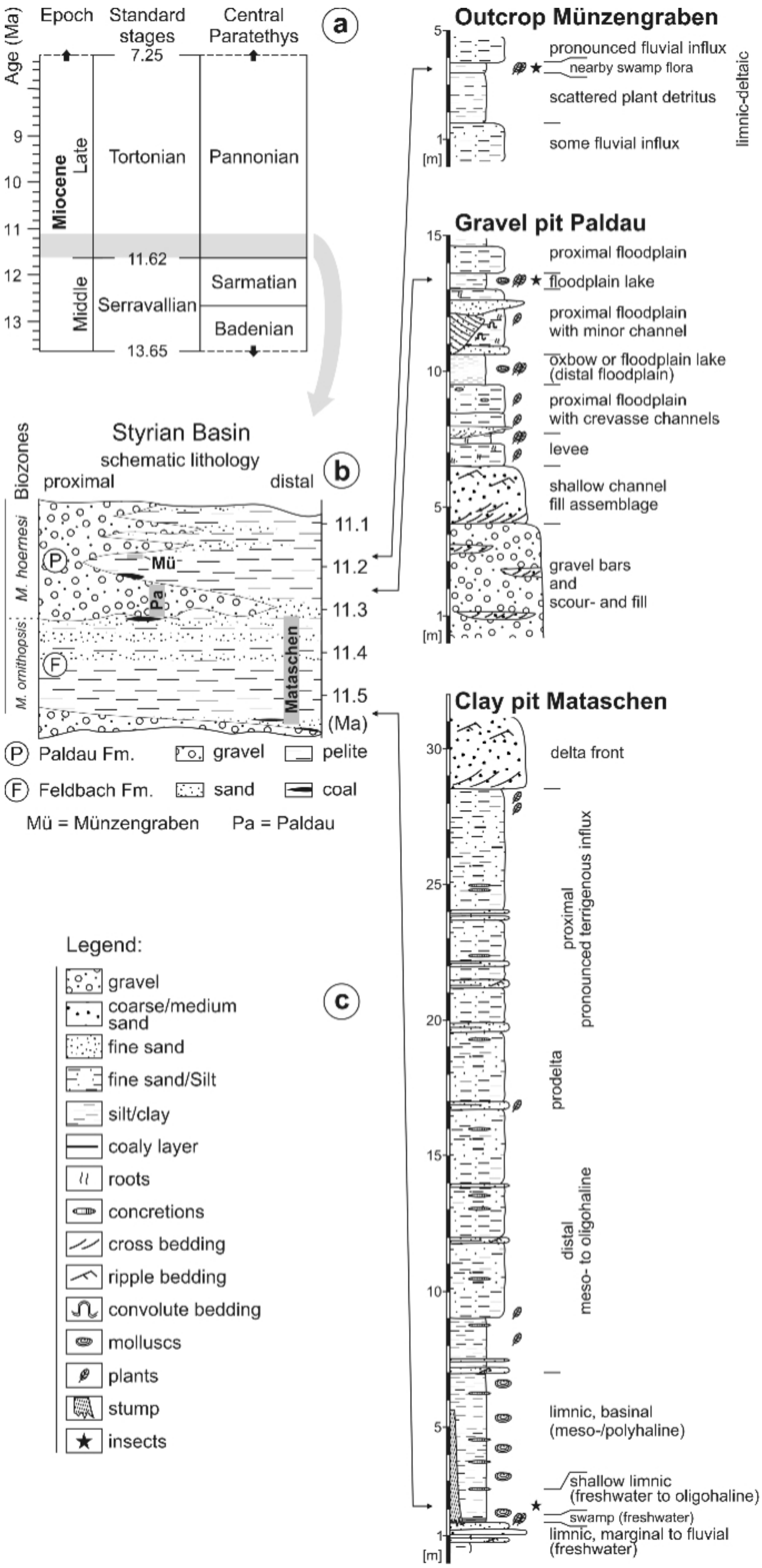

Figure 2: Stratigraphy, profiles, and facies interpretation of the Pannonian insect localities of Styria. (a) Correlation of Standard and Central Paratethys stages. (b) Litho- and biostratigraphical scheme of Lower Pannonian sediments in the Styrian Basin. (c) Profiles and proposed sedimentary environment.

largely dominated by extinct taxa from the Cretaceous, with relatively few Cenozoic or modern survivors. The specimen represents a new genus which can be excluded from the aforementioned three families and is most likely representative of the stem lineage to the latter three genera (Engel and Gross, in press). Perhaps most interesting of all is the prodigious size of the forewing. At 33.5 mm in length it is the largest fossil termite wing and among the largest of all members of the order, rivaled only by the Neotropical giants of the derived genus Syntermes (Termitidae: Syntermitinae) (Engel and Gross, in press).

Order COLEOPTERA Linnaeus, 1758

Several remains, mostly isolated elytra, are attributable to beetles. In total at least five distinctive morphospecies of beetles can be identified from the three deposits (Fig. 3b–f).

Specimen LMJ 204.157 from Mataschen is a poorly preserved elytron of a large beetle (Fig. 3b), with a maximum preserved length of 19.9 mm and width of 6.8 mm. The elytron has at least 17 striae composed of small, deep punctures in single, irregularly spaced rows. The integument between the striae is apparently relatively flat and imbricate, and the overall structure of the elytron is relatively flat, with the lateral margin being weakly convex before tapering quickly posteriorly in its apical quarter.

Specimen LMJ 204.153 from Paldau is the basal portion of a relatively large and robust beetle abdomen, preserved with the sterna exposed (Fig. 3c). The maximum length of the abdominal fragment is 9.3 mm and the width 11.1 mm. The sterna are relatively smooth to very faintly imbricate and with widely scattered, small but deep punctures. The punctures are more dense basally (separated by 1–5 times a puncture width) and pro-

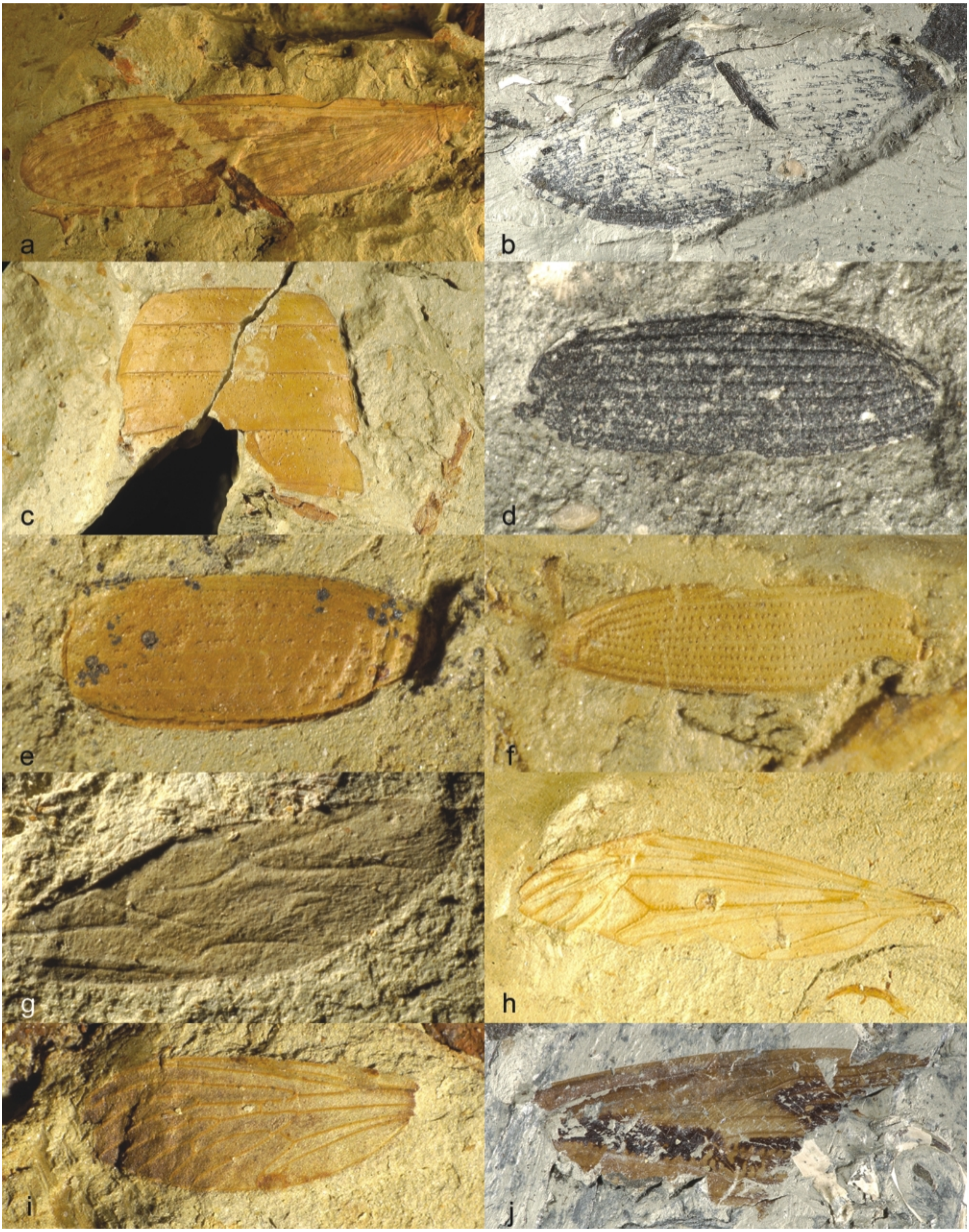

Figure 3: Representative diversity of Pannonian-age insects from Styria. (a) A new genus and species of giant termite (Isoptera), Paldau, LMJ 204.149 (wing length 33.5 mm). (b) Elytron of an indeterminable family of beetles (Coleoptera), Mataschen, LMJ 204.157 (elytron length 19.9 mm). (c) Abdominal sterna of an indeterminable beetle (Coleoptera), Paldau, LMJ 204.153 (length of abdomen 9.3 mm). (d) Elytron of a ground beetle, perhaps near *Pterostichus* (Coleoptera: Carabidae), Mataschen, LMJ 201.116 (elytron length 7.7 mm; specimen originally reported by Gross, 2004a). (e) Elytron of a ground beetle (Coleoptera: Carabidae), Paldau, LMJ 204.154 (elytron length 7.5 mm). (f) Elytron of a possible donaciine leaf beetle (Coleoptera: Chrysomelidae), Münzengraben, LMJ 204.156 (elytron length 7.1 mm). (g) A formicine ant forewing (Hymenoptera: Formicidae), Paldau, LMJ 204.150 (wing length 14.3 mm). (h) A new species of crane fly, genus *Tipula* (Diptera: Tipulidae), Paldau, LMJ 204.151 (wing length 18.7 mm). (i) A generalized brachyceran fly wing, perhaps of the snipe fly family Rhagionidae (Diptera: Brachycera), Paldau, LMJ 204.155 (wing length 6.7 mm). (j) A large caddisfly perhaps allied to the genus *Agrypnia* (Trichoptera: Phrygaenidae), Mataschen, LMJ 204.158 (wing length 20.1 mm).

gressively more sparse on the sternal discs (separated by 3–12 times a puncture width). Sterna I–IV are preserved, with a tiny fragment of the right extreme base of sternum V. Although likely some kind of polyphagan beetle, assignment as to family is not possible.

Specimen LMJ 201.116, from Mataschen, is a complete ground beetle elytron (Carabidae), somewhat similar to the genus *Pterostichus* (Fig. 3d), and was initially reported by Gross (2004a). The specimen has a maximum length of 7.7 mm and width of 2.8 mm. The elytral surface bears eight striae composed of small, shallow, relatively regularly and closely spaced punctures. The intervals between the striae are imbricate and impunctate, and not raised. The outer margin is very weakly convex for most of its length before tapering more strongly in the apical third to what was apparently a rounded apex, the apex being only very weakly deflected.

Specimen LMJ 204.154 is a complete elytron from Paldau of a possible ground beetle (Carabidae) (Fig. 3e). The elytron has a maximum length of 7.5 mm and width of 3.2 mm, with eight striae composed of small, deep punctures in single rows and irregularly spaced, usually in sets of three or two. The intervals between the striae are somewhat swollen and the integument imbricate, impunctate, and apparently weakly rugulose. The outer margin is roughly parallel to the mesal sutural margin for two-thirds of the elytral length before gently tapering to a relatively acutely rounded apex which is gently deflected.

Specimen LMJ 204.156, from Münzengraben, is a nearly complete beetle elytron, likely of the leaf beetle subfamily Donaciinae (Chrysomelidae) (Fig. 3f). The elytron is missing the posterio basal section but is otherwise largely complete with a length of 7.1 mm and width of 2.1 mm. The elytron has nine striae composed of well-defined, regular, small punctures, some striae converging and merging posteriorly near the acutely rounded apex. The intervals between the striae are relatively flat, imbricate, and impunctate.

Specimen LMJ 204.152 represents what is perhaps an abdominal and basalmost thoracic fragment of a robust adephagan beetle, but is otherwise too fragmentary to permit confident attribution. Attribution to Adephaga is suggested by what appears to be the preserved impression of the metacoxae overlapping and "dividing" the first abdominal sternum. In addition, the second through fifth abdominal sterna are preserved. The abdomen appears broad, with convex lateral margins and concave posterior sternal margins, which become progressively more concave toward the apex. The integument is apparently imbricate and the abdominal spiracles distinct laterally. The maximum length is 6.8 mm and the width 8.2 mm.

Order HYMENOPTERA Linnaeus, 1758

From the Paldau site has been recovered the forewing of a formicine ant (LMJ 204.150). The wing is relatively faintly impressed and is missing the basalmost section (Fig. 3g) but the venation can otherwise be easily reconstructed (Fig. 4a). The wing as preserved has a maximum length of 14.3 mm and a width of 4.8 mm. Placement of the wing is challenging and there have been few works evaluating the systematic value of ant wing venation (Brown and Nutting, 1949). There is some resemblance to the myrmicine genus *Aphaenogaster*, particularly those previously classified as *Novomessor*, with a single species described from the Pannonian of the Vienna Basin (Bachmayer, 1960). However, in *Aphaenogaster pannonicus* Bachmayer a distinct discoidal cell is present, the apical abscissae of Rs and M do not converge at or join distal to the r-rs crossvein (instead M diverges well prior to r-rs), and the marginal cell is open (*i.e.*, Rs does not terminate on the wing margin). Moreover, in most *Aphaenogaster* the distal abscissae of Rs and M converge to a cross with Rs+M and r-rs (*i.e.*, there is no Rs+M stem beyond r-rs) and the marginal cell is open or Rs weakens near the apex. Instead, the venation is more indicative of some Formicinae such as *Pseudolasius*, *Brachymyrmex*, *Camponotus*, and *Phasmomyrmex* among others (Brown and Nutting, 1949). While the forewing venation is strongly reminiscent of some ants of the genus *Camponotus*, a diverse group today occurring throughout the world, including Austria, there is rarely a Rs+M stem distal to r-rs. Fossils of *Camponotus* are well documented from the Cenozoic of North American and Eurasia (e.g., Carpenter, 1992; Bolton, 1995). Until additional material has been recovered we prefer to consider the current isolated and incomplete forewing as simply an undetermined formicine.

Given the abundance of parasitoid wasps of the Ichneumonoidea in some Cenozoic sites (e.g., the Florissant shales of Colorado, USA), it is surprising that an ichneumonoid has not yet been discovered at Paldau. Indeed, further excavations at Pannonian sites in Styria may very well reveal more hymenopteran specimens as this order is relatively abundant in other Neogene sites of Europe.

Order DIPTERA Linnaeus, 1758

Two species of true flies have been recovered, both from the Paldau locality and representing both suborders of Diptera. Specimen LMJ 204.151 is that of an essentially complete crane fly forewing (Tipulomorpha: Tipulidae) represented by part and counterpart, although the counterpart is missing the apical half of the wing. The maximum length of the wing as preserved is 18.7 mm, with a maximum width of 4.9 mm. The wing has undergone some deformation during preservation such that the apical fourth is slightly crumpled and folded transversely, setting the apicalmost portion off at an oblique angle relative to the remainder of the wing (Fig. 3h). The venation is detailed in figure 4b, with the apical portion straightened as it would have been in life, although owing to the damage as preserved the space between veins M_3 and CuA_1 is missing. The crane flies represent the basalmost lineage of Diptera, and whose larvae are saprophagous and generally live in wet soil or mud. They are well documented in the fossil record, particularly the genus *Tipula* which has over 75 species described from the Cenozoic of North America and Eurasia (e.g., Evenhuis, 1994).

The other fly (LMJ 204.155) is a generalized brachyceran forewing, missing the basalmost portion and ampulla (Fig. 3i). The maximum length as preserved is 6.7 mm, with a maximum width of 2.6 mm. Placement as to suborder is easily made by the meeting of CuA_2 and A_1 at posterior wing margin (Fig. 4c). No subcostal break is evident and neither is a sc-r crossvein. The venation is reminiscent of some snipe flies (Rhagionidae) given the placement of R_5 just posterior to the wing apex and there is some similarity with species of the genus *Rhagio*. However, such a placement cannot be made with certainty.

Order TRICHOPTERA Kirby, 1813

Specimen LMJ 204.158 is a fragmentary forewing of a phrygaenid caddisfly from Mataschen (Fig. 3j). The apical portion of the wing has been torn away as have the base and posterior margin, with only a small section of Cu_2 remaining of the latter. The preserved fragment has a maximum length of 20.1 mm and width of 8.1 mm. Fortunately sufficient venational details remain to make a confident placement as to family. Indeed, the venation (Fig. 4d) is reminiscent of the genus *Agrypnia*, the largest genus of Phrygaenidae and of Holarctic distribution. Phrygaenids typically live in ponds or wetlands and the larvae construct cases out of plant material arranged in a spiral or ring, a general biology fitting with our understanding of the Mataschen environment.

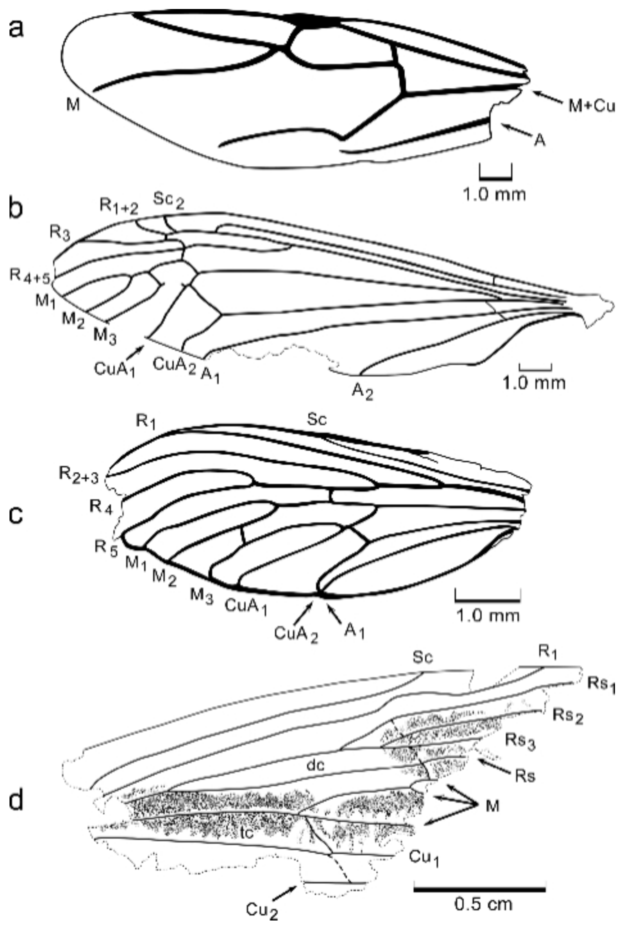

Figure 4: Forewing venations of four insects from the Pannonian of Styria. (a) A winged ant (Formicidae) likely of the Formicinae (LMJ 204.150). (b) A new species of crane fly (Tipulidae: *Tipula* sp.) (LMJ 204.151). (c) A generalized brachyceran fly, perhaps a snipe fly (Diptera: Rhagionidae?) (LMJ 204.155). (d) A phrygaenid caddisfly, perhaps near the genus *Agrypnia* (Trichoptera: Phrygaenidae) (LMJ 204.158) (dc = discoidal cell; tc = thyridium cell).

4. Discussion

Several authors mentioned the high potential for further insect findings in Pannonian fine clastics regardless of their fluvial, deltaic, or limnic origin (e.g., Papp and Mandl, 1951; Schlüter, 1979). Certainly this statement is not only true for this time interval. Nevertheless, insect remains seem to be largely overlooked or even neglected during paleontological sampling campaigns. While insects are a critical force in modern and past ecosystems, our fundamental knowledge of their fossil record, while better than most entomologists realize, remains to be fully explored or documented (Grimaldi and Engel, 2005). Conclusions regarding their Cenozoic diversity, evolution, paleoecological impact (ranging from plant–insect interactions, their role in the food chain, recycling of organic matter, taphonomy, etc.), and paleoclimatic implications are still hampered by poor sampling of suitable deposits, or basic systematic evaluation of those sizeable samples already recovered in some regions of the world. The fragmentary nature of the remains limits the interpretation of the biogeographic implications of these insects. Nearly all of the material consists of isolated forewings, or two fragmentary abdomens of beetles, thereby lacking critical information from the remainder of the anatomy. For two species sufficient taxonomic information is present in the forewing (*i.e.*, the termite and crane fly), but the genus *Tipula* is widespread in a diversity of habitats including modern Styria while the termite is representative of a primitive grade that has subsequently become extinct but is similarly found in a diversity of habitats. Nonetheless, the termite is certainly suggestive of a significantly warmer climate necessary to support colonies of such large species, analogous to the distribution of giant termites (albeit of unrelated genera) today in Australia or South America. The isolated beetle elytra cannot be definitively assigned, although several appear to be ground beetles, common in modern Europe and frequently found in a diversity of habitats including along the edges of ponds, lakes, or in riparian zones, similar to the caddisfly also reported herein. Certainly much further work is necessary and continued excavations will hopefully reveal more complete material in addition to the isolated wings. While we document representatives of only five of 30 extant insect orders, with this brief overview we hope to stimulate others to take a more careful look in these and other deposits for this ubiquitous lineage of animals.

Acknowledgements

We are grateful to M. Harzhauser and T. Wappler for critical reviews on the manuscript that improved the final draft, to D. Grimaldi for thoughts on the generalized brachyceran, and to S. Elias for identifications of the isolated beetle elytra. Partial support for this project was provided by National Science Foundation, USA grants EF-0341724 and DEB-0542909 (to M.S.

Engel). Line drawings of the wing venations were executed by S. Taliaferro, supported by the Engel Illustration Fund of the University of Kansas. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum and the Department of Geology and Palaeontology of the Landesmuseum Joanneum.

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Received: 24. October 2008
Accepted: 19. November 2008

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