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**Two new odonate-like insect wings
from the latest Norian of northern Germany**

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ABSTRACT. Two new well preserved odonate (damsel-dragonflies) insect wings from the latest Norian (Upper Triassic) of two different localities are described. Although the rather long distance of more than 250 km separates the localities, the holotypes occur in comparable lithologies and are thus described together. We describe an odonate forewing, *Italophlebia baueri* sp. n., from an abandoned quarry at Langenberg near Seinstedt north of the Harz Mountains (Lower Saxony), which is the first occurrence of this genus outside Italy. The second wing, *Triassothemis gartzii* sp. n., was found in the cored well Gartz 1 (NE Germany). In both occurrences the insect wings were associated with abundant autochthonous as well as allochthonous faunal and floral remnants of shallow subaqueous environments.

KEY WORDS: *Triassothemis*, *Italophlebia*, Palaeodictyoptera, Odonata, Triassolestidae, insect wing, Late Triassic, Germany.

INTRODUCTION

Italophlebia baueri sp. n. and *Triassothemis gartzii* sp. n. were found in Keuper sediments of late Triassic age. As the Keuper strata in the Central European Basin (CEB) comprises predominantly terrestrial deposits often intensely modified by pedogenic processes, remnants of insects, especially wings, are rarely found. On a global scale environmental changes at the Permian/Triassic boundary are considered as a major impact on

the development of insects. SHCHERBAKOV (2008b) stated that the entire class of insects was strongly reduced in diversity at the P/T boundary. After recovery the post-Permian insect fauna already contained many elements common to modern insects (LABANDEIRA & SEPkoski 1993, LABANDEIRA & EBLE 2000, BÉTHOUX et al. 2005 and others). The oldest representatives of many groups are first recorded in the Triassic (Grilloblattodea, Titanoptera, Phasmatodea, Hymenoptera). However, even on a global scale insects are rarely recorded, and findings are restricted to freshwater deposits of lakes and floodplains. To date, insects from the Triassic of the CEB have been described e.g. from Germany (BRAUN 1860, HANDLIRSCH 1912, LANGE 1923, ZEUNER 1930, KUHN 1937, 1938 a, b, MÜLLER 1965, BRAUCKMANN & SCHLÜTER 1993, ANSORGE 1994, ANSORGE & BRAUCKMANN 2008, WILLMANN 2008), France (GALL 1971, PAPIER et al. 2005, GALL & GRAUVOGEL-STAMM 2005) and Poland (ŻYŁA et al. 2013). Overviews of Triassic insect localities are provided by SCHLÜTER (2003) and SHCHERBAKOV (2008a).

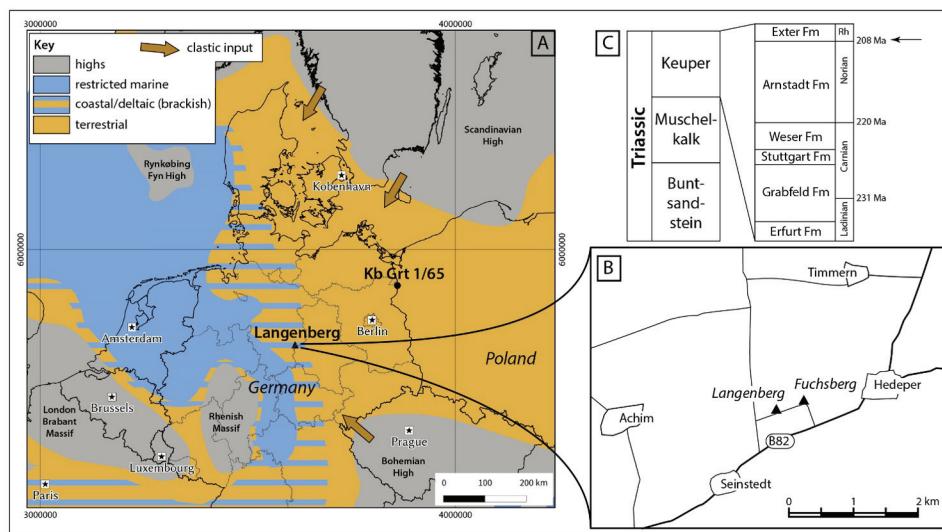


Fig. 1. A – Simplified early Rhaetian palaeogeography of the Central European Basin with positions of the Langenberg outcrop and the Gartz 1 cored well, modified after FISCHER et al. (2012); B – Close-up showing the detailed locations; C – Triassic and Keuper stratigraphy in the CEB, compiled after DSK (2005). The arrow marks the horizons of the find.

Geological setting and locations

The epicontinental CEB stretched from today's eastern United Kingdom to eastern Poland and from southern Scandinavia to northern Switzerland (Fig. 1). In late Triassic

times it was situated at palaeolatitudes between 35° and 50°N (STAMPFLI & KOZUR 2006) and bordered by the British-Scandinavian Caledonides and the Fennoscandian High to the north and remnants of the former Variscan orogeny to the South (ZIEGLER 1990).

The typical late Triassic Keuper basin fill is characterized by variegated shaly lithologies of terrestrial Playa-like to Sabkha-like environments (NITSCH 1995, REINHARDT & RICKEN 2000). Intense modification of shales by pedogenic processes is a common feature and the sedimentation of coarse-grained siliciclastics was limited to basin margins (FRANZ 2008). Short-term ingressions through gates to the south and south-east were mainly limited to southern parts of the CEB (BACHMANN et al. 2010).

Related to the break-up of Pangaea, the intensified rifting at the western margins of the CEB opened new gates in latest Norian–earliest Rhaetian times and the transgression of a shallow inland sea changed the palaeogeography fundamentally (Fig. 1). Successively the ‘Rhaetian Sea’ spread across the CEB from west to east and replaced terrestrial environments with restricted marine to coastal ones. In its maximum flooding stage the Rhaetian Sea extended to the eastern parts of Germany (FISCHER et al. 2012). Later, in Jurassic times, the transgressive trend culminated in fully marine environments throughout larger parts of the CEB.

Around the Norian-Rhaetian boundary the early Rhaetian Sea stretched from the eastern United Kingdom as far as the western parts of Germany. A belt of coastal-deltaic environments trended from westernmost Denmark down to central Germany and separated the shallow marine environments of the western CEB from the terrestrial ones of the eastern CEB (Fig. 1).

Italophlebia baueri sp. n. was found within a 1 m thick fossiliferous layer that is part of an almost 8 m thick succession exposed in the abandoned quarry at Langenberg (Fig. 2). The section is composed of sandstones, siltstones and claystones, and reconstructions of the depositional environment vary from restricted marine (BENDA 1960, 1963) to fluvial (APPEL 1981, HAUSCHKE & WILDE 1996). Several fossiliferous layers at Langenberg and Fuchsberg give considerable insights into palaeoenvironments. SCHLÖNBACH (1861) and PFLÜCKER Y RICO (1868) reported fish remains, ganoid scales and bivalves, and BRAUNS (1866) described the floral assemblage. A bone fragment of the prosauropod *Plateosaurus* was mentioned by FRAAS (1897). HAUSCHKE & WILDE (1987, 1996) provided a first synopsis of the fauna and described insects, limulids (the holotype of *Paleolimulus fuchsbergensis*), conchostracans, semionontid-like fishes, coelacanthid scales and malacostracan crustaceans. Conchostracans were described by BARTH & KOZUR (2011) and HAUSCHKE & KOZUR (2011). To date, nine insect orders are known from the localities at Fuchsberg and Langenberg: Coleoptera, Odonata, Diptera, Hymenoptera, Ephemeroptera, Blattodea, Orthoptera, Mecoptera and Hemiptera (BARTH 2011).

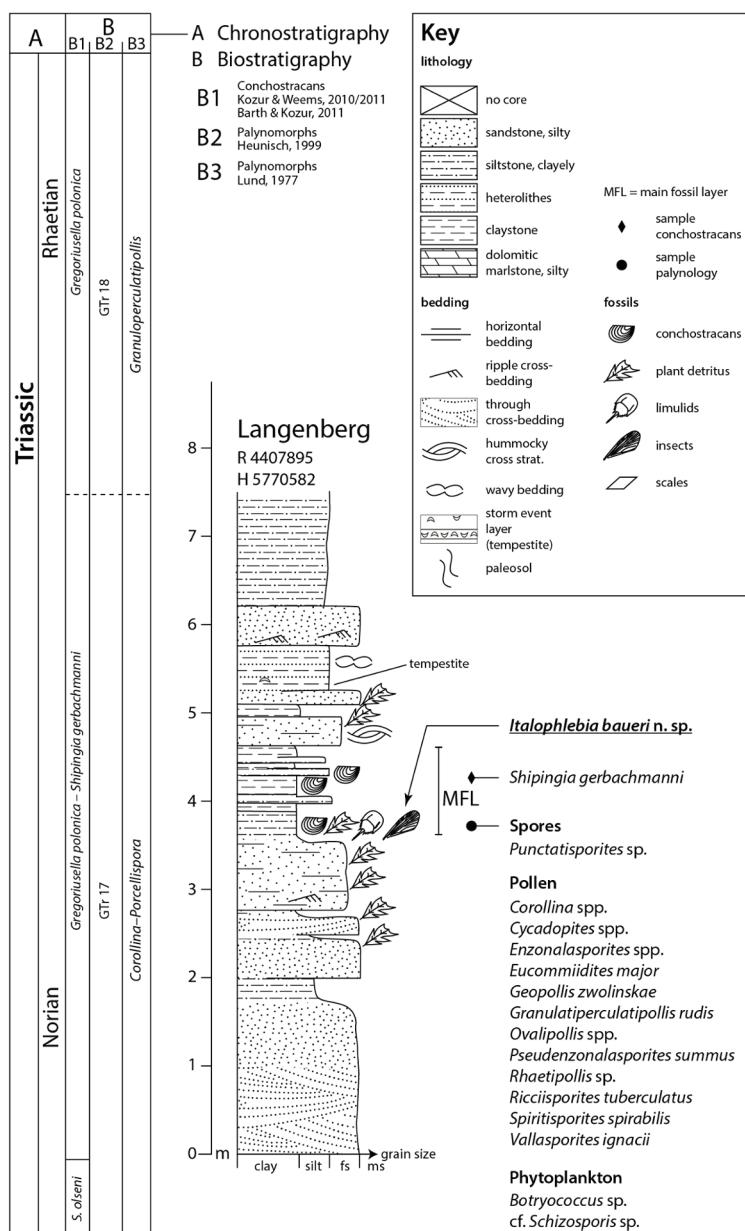


Fig. 2. Sedimentological log of the exposed section at Langenberg. *Italocephelia baueri* sp. n. was found in the fossiliferous layer, the so-called ‘Main Fossil Layer’ in the middle part of the section. See Fig. 1 for location of outcrops.

The first occurrence of the genus *Ipsvicia* outside of Gondwana has been described from Langenberg (BARTH et al. 2011). Recent analyses of the palynology of the fossiliferous layer revealed typical sporomorph assemblages dominated by terrestrial spores and pollen. In addition, subordinated occurrences of *Botryococcus* sp. and *Schizosporis* sp. have been recorded at Langenberg and *Leiosphaeridia* sp. and *Tassmanites* sp. at Fuchsberg (HEUNISCH 1998, 2011a, b). Together, the recorded fauna and the presence of aquatic phytoplankton may suggest a subaqueous coastal environment with a brackish influence.

Triassothemis gartzii sp. n. was found at 1083.65 m depth in the Gartz 1 cored well (Fig. 3). The finding layer is part of an almost 25 m thick monotonous interval of greyish shales ranging in depth from 1070 to 1095 m that are assigned to the late Triassic Lower Exter Formation. The shales commonly show horizontal lamination and comprise abundant plant detritus, fish scales and in parts conchostracans. In the upper part thin siltstone layers are interbedded and towards the top the shales have been modified by pedogenic processes. Lithofacies and biofacies argue for a freshwater lake that was part of a larger Playa-like system (FRANZ 2008).

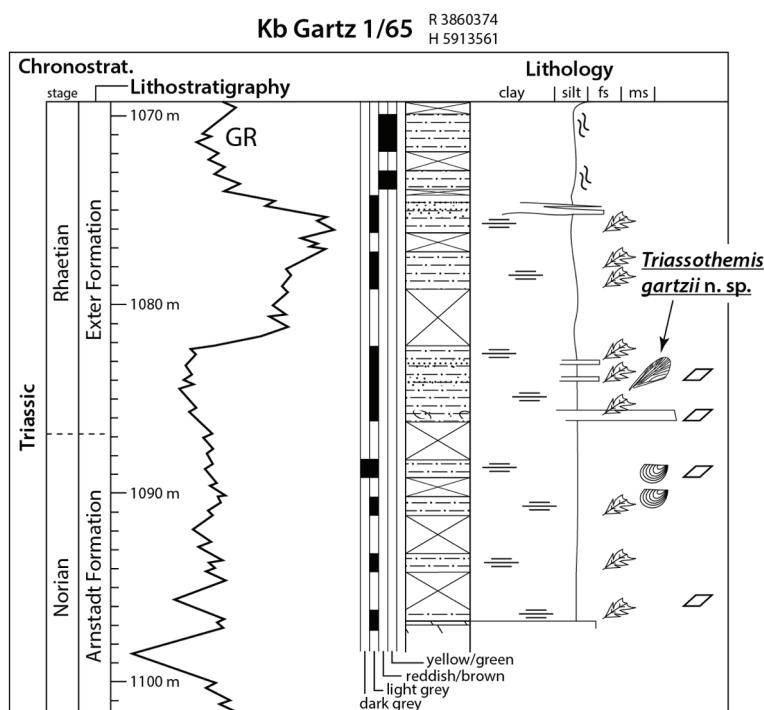


Fig. 3. Sedimentological log of the Gartz 1 cored well from 1070-1100 m depth. *Triassothemis gartzii* sp. n. was found at 1083.65 m depth. See Fig. 1 for the borehole location and Fig. 2 for the key. GR = gamma ray log, fs = fine grained sandstone, ms = medium grained sandstone.

Stratigraphic age

Age control of terrestrial to restricted marine late Triassic strata in the CEB is mainly provided by zonations based on palynomorphs and conchostracans (LUND 1976, 1977, HEUNISCH 1996, KOZUR & WEEMS 2007, 2010, 2011). *Italophlebia baueri* sp. n. was found within a fossiliferous layer where it co-occurred with *Shipingia gerbachmanni*, the guide form of the latest Norian *gerbachmanni* zone (HAUSCHKE & KOZUR 2011, BARTH & KOZUR 2011). *Shipingia gerbachmanni* was also found in correlative strata of the neighbouring outcrop at Fuchsberg (BARTH 2011). In the uppermost part of the succession exposed at Fuchsberg the guide form of the early Rhaetian *gregoriusella* zone *Gregoriusella polonica* indicates an early Rhaetian age and enables a fairly precise drawing of the Norian–Rhaetian boundary (BARTH & KOZUR 2011). However, the correlative strata are not exposed at Langenberg. Taking both outcrops together the fossiliferous layer at Langenberg can be considered of latest Norian age slightly below the base Rhaetian.

The sporomorph assemblage of the fossiliferous layer at Langenberg comprises *Granuloperculatipollis rufus*, *Ricciisporites tuberculatus*, *Enzonalsporites* spp., *Rhaetipollis* sp. and other taxa that range from the late Norian to early Rhaetian. A more precise assignment is not possible because of the limited number and preservation of sporomorphs, but a latest Norian age close to the base Rhaetian appears most likely.

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Abbreviations

A – Analis, Arc – Arculus, C – Costa, Cu – Cubitus, CuA – Cubitus anterior, IR – Interradius, MA – Media anterior, MP – Media posterior, N – Nodus, Pt – Pterostigma, R – Radius, RA – Radius anterior, RP – Radius posterior, Sc – Subcosta.

SYSTEMATIC PALAEONTOLOGY

Order: Odonata

Family: Triassolestidae TILLYARD, 1918

Genus: *Triassothemis* CARPENTER, 1960

Triassothemis gartzii sp. n.

(Figs 4A-C)

Material

Holotype specimen, which will be stored in the collection of the Geologic State Survey Brandenburg (Landesamt für Bergbau, Geologie und Rohstoffe, LBRG); at present uncatalogued.

Age and outcrop

Cored well Kb Gartz 1/65, grey siltstones from the Norian-Rhaetian boundary interval, depth = 1083.65 m, cored box nr. 677.

Etymology

Named after the cored well Kb Gartz 1/65.

Description

Part and counterpart of a wing fragment, with basal section up to the discoidal cell and extreme apex missing, dark brown, preserved section 19.5 mm long, 6.2 mm wide, distance from MAb to nodus N 5.5 mm, from N to wing apex 1.4 mm, from N to Pt 7.5 mm, from Pt to wing apex 5.0 mm; Pt poorly preserved but certainly present because of wider RA below it, parallel sided narrow elongate, ~2.5 mm long, ~1.0 mm wide, covering two cells, pterostigmal brace not clearly visible, probably weakly oblique; antenodal area not preserved. No cross-vein between RA and RP basal of base of RP3/4 and one opposite this point obliquely slanted towards apex between RA and RP; no visible nodal break in costal margin, ScP progressively fused with costal margin in N, along the anterior edge of the first postnodal cell; nodal crossvein perpendicular to costal margin and RA, subnodus very slightly oblique, longer than nodal crossvein and not exactly aligned with it; seven postnodal crossveins between N and Pt, aligned with seven postsubnodal crossveins between RA and RP; base of RP3/4 one cell basal of subnodus, base of IR2 $\frac{3}{4}$ of a cell distal of subnodus; base of RP2 three cells distal of subnodus, base of IR1 seven cells distal of base of RP2, below proximal part of Pt; longitudinal parts of RP3/4, IR2, RP2 and IR1 distinctly closer to longitudinal vein below it than to main stem of RP, so that these veins apparently do not emerge from stem of RP; no oblique vein 'O' between IR2 and RP2; areas between IR1 and RP2, RP2 and IR2 and IR2 and RP3/4, RP3/4 and MA all distally greatly widened, those between RP2 and IR2 and RP3/4 and MAa with six secondary parallel veins apparently emerging from RP2 and RP3/4 respectively and going to posterior wing margin; RP2 and IR2 anteriorly curved while RP3/4 and MAa posteriorly curved in their distal parts; IR2, RP3/4 and MAa basally straight; only distal side MAb of discoidal cell preserved, very long, 1 mm long, oblique; postdiscoidal area with one row of cells, basally broad, narrower then broader again and narrower along posterior wing margin; CuA and MP separating exactly at distal end of MAb; MP slightly curved; CuA weakly zigzagged; one row of cells in areas between MP and CuA and CuA and posterior wing margin.

Discussion

Even though the anal area is not preserved, this fossil is very similar to the genus *Triassothemis* CARPENTER, 1960 (Isophlebioptera: Parazygoptera: Triassolestidae) (CARPENTER 1960). According to its general shape, this fossil is a forewing. It shares the following synapomorphies with the Isophlebioptera BECHLY, 1996: space between RP3/4 and MA distinctly expanded and traversed by several pectinate convex ‘secondary branches’ of RP3/4; postdiscoidal space between MP and MA narrow with only one row of cells between them; CuA postero-distally indistinct (zigzagged), distal space between MP and CuA strongly expanded. The absence of intercalary veins between IR1 and RP1, IR1 and RP2, and RP3/4 and IR2 would exclude affinities with the Euthemistidae PRITYKINA, 1968 and the Sphenophlebiidae BECHLY, 1997. The RP2 arising distinctly distal of subnodus is the synapomorphy of the Parazygoptera BECHLY, 1997. The absence of an antefurcal crossvein in the space between RP and MAA basal of RP3/4 (midfork) is the apomorphy of the Euparazygoptera BECHLY, 1997. The two characters ‘IR2 and MAA not distally zigzagged’ and ‘base of IR2 distal of subnodus’ exclude affinities with the Asiopteridae PRITYKINA, 1968. The distally narrow postdiscoidal area and the greatly expanded area between RP3/4 and MAA exclude affinities with the Cyclothemistidae BECHLY, 1996 (*Cyclothemis* PRITYKINA, 1980, *Shurabiola* PRITYKINA, 1980, *Sogutella* PRITYKINA, 1980, and *Pseudotriassothemis* BECHLY, 1997). The Mesophlebiinae TILLYARD, 1916 are excluded because the postnodal part of the wing is not shortened, MA is not distally zigzagged, the base of IR2 is distal of the subnodus, the postdiscoidal area has only one row of cells and there are no supplementary veinlets in its distal part (TILLYARD & DUNSTAN 1916).

This fossil shares the following synapomorphies with the Triassolestinae TILLYARD, 1918: nodal crossvein and subnodus perpendicular to RA, and more or less aligned; a distinctly oblique crossvein basal of subnodus obliquely slanted towards apex between RA and RP. The following synapomorphies of the Triassothemistini FUJIYAMA, 1991 are present in *Triassothemis gartzii* sp. n. (FUJIYAMA 1991, BECHLY 1997), but not in the Triassolestini TILLYARD, 1918: MA and MP distinctly converging near hind margin; area between RP3/4 and MA basally rather narrow for a considerable distance; area between IR2 and RP3/4 basally very narrow, then expanded, and distally again narrowed; area between RP2 and IR2 basally very narrow (TILLYARD 1918, RIEK 1976, PRITIKINA 1980, 1981). The Triassothemistini comprise the genera *Triassothemis* CARPENTER, 1960 (*Triassothemis* *Triassothemis mendozensis* CARPENTER, 1960, *Triassothemis* *Afrotriassothemis heidia* RIEK, 1976, *Triassothemis* *Afrotriassothemis regularis* RIEK, 1976) and *Italophlebia* WHALLEY, 1987 (*Italophlebia* *gervasutti* WHALLEY, 1987, *Italophlebia* *paganoniae* BECHLY, 1997, *Italophlebia* *baueri* sp. n. (see below and BARTH 2011)).

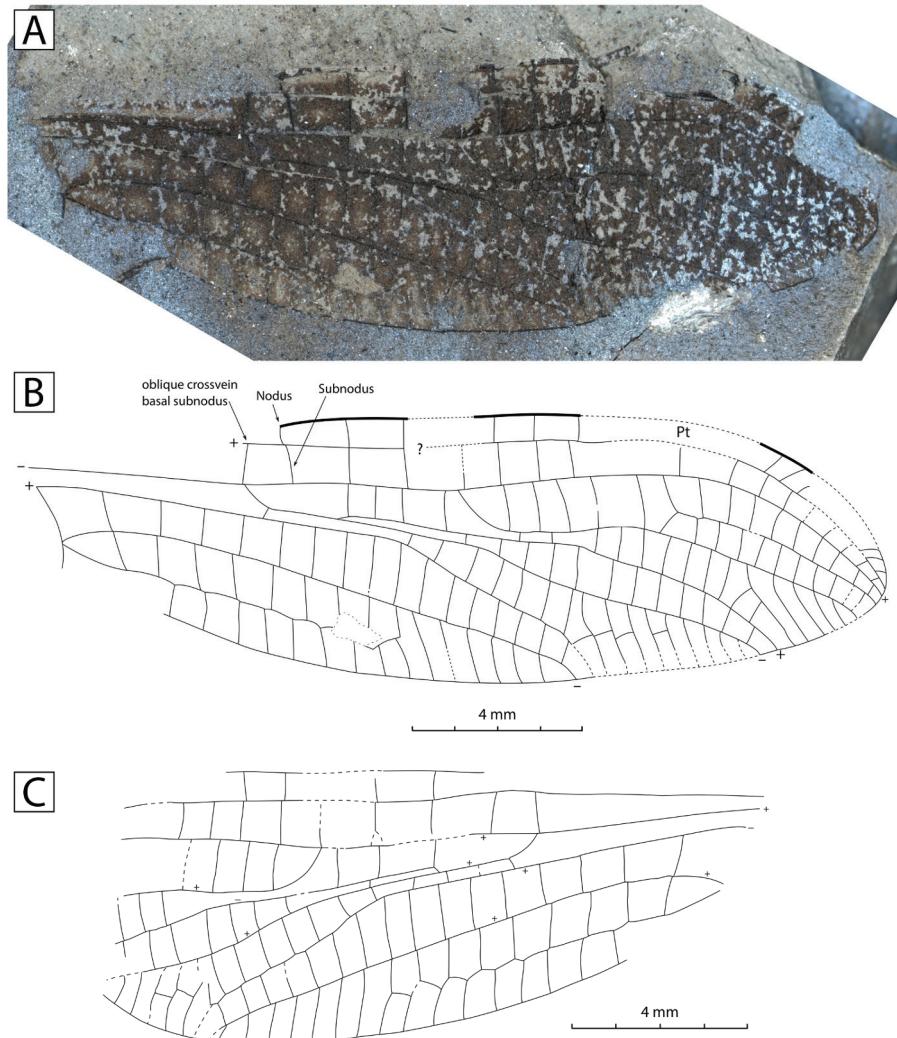


Fig. 4. Photograph and venation drawing of print (A+B) and counterprint (C) of *Triassothemis gartzii* sp. n. Holotype, cored well Gartz 1 (Brandenburg, Germany), latest Norian, depth = 1083.65 m. For abbreviations, see above.

After BECHLY (1997), distinct autapomorphies of *Italophlebia* are the distally strongly converging veins RP1 and RP2, the distally zigzagged vein MA, and the shortened and zigzagged IR1. Autapomorphies of the subgenus *Afrotriassothemis* BECHLY, 1997 are the numerous cells below the elongated pterostigma, very long and straight IR1, RP2

and IR2 basally very close together for a longer distance, and two rows of cells between the distal parts of IR2 and RP3/4. These characters are not present in *T. gartzii* sp. n., which, on the other hand, has a Pt covering only two cells, as in *Triassothemis mendozensis*.

T. gartzii sp. n. differs from *Triassothemis mendozensis* (and from the other Triassothemistini, except perhaps *Triassothemis Afrotriassothemis heidiae* in which the bases of IR2 and RP3/4 are not clearly preserved), in the distal positions of IR1, RP2, and IR2, all well distal of subnodus. These differences justify attribution to a new species, but not to a new genus.

Affinities with *Triassophlebia stigmatica* TILLYARD, 1922, a putative Parazygoptera, are unlikely because of the shorter Pt, and the very different pattern of the areas between the main veins in the distal part of the wing. *Triassophlebia* is based on a very incomplete fossil wing (TILLYARD 1922, JELL 2004).

Genus: *Italophlebia* WHALLEY, 1987

Italophlebia baueri sp. n.

(Figs 5A-C)

Material

Holotype specimen MLU.Sei2010.253a+b (part and counterpart of a fore wing), stored in the palaeontological collection of the Institute of Geology, Martin-Luther-University, Halle-Wittenberg, Germany.

Age and outcrop

Latest Norian ('Main Fossil Layer', BARTH & KOZUR 2011), abandoned quarry at Langenberg near Seinstedt, Lower Saxony, Germany).

Etymology

After the collector, Kathleen Bauer (Naturmuseum Südtirol, Bozen, Italy).

Description

Print and counterprint of a nearly complete fore wing, with extreme base and postero-apical margin missing; wing 32.5 mm long, 6.0 mm wide; distance from base to arculus 5.5 mm, from arculus to nodus 11.25 mm, from nodus to wing apex 14.25 mm, from nodus to pterostigma 8.75 mm; upper margin of costa near N slightly folded; C up to this point simply convoluted; AA straight in basal part and posteriorly curved distally; MP+Cu parallel to AA at wing base, distally defining a rather broad subdiscoidal space; CuP not preserved; at acute distal angle of discoidal cell, MP+CuA fused with AA, CuA+AA separating from MP slightly distally; one row of cells in area between CuA(+AA) and posterior wing margin, 1.0 mm wide; discoidal cell basally opened; arculus aligned with MAb in a straight oblique vein. A very open angle between MAa and MAb;

postdiscoidal area broad but strongly narrowed near posterior wing margin and with only one row of narrow cells; MAa nearly straight up to level of nodus, deformed distally, but weakly zigzagged; base of RP3/4 8.0 mm from arculus and 2.9 mm from subnodus, that of IR2 9.75 mm distally; base of RP2 3.25 mm distal of nodus, that of IR 15.25 mm distally; IR1 apparently emerging from RP2; RP3/4 and IR2 strongly approximate in their basal parts, but diverging significantly in distal halves; RP1 and RP2 distally strongly converging; Pt dark brown, 2.25 mm long, 0.75 mm wide, covering two cells, pterostigmal brace present but weakly oblique.

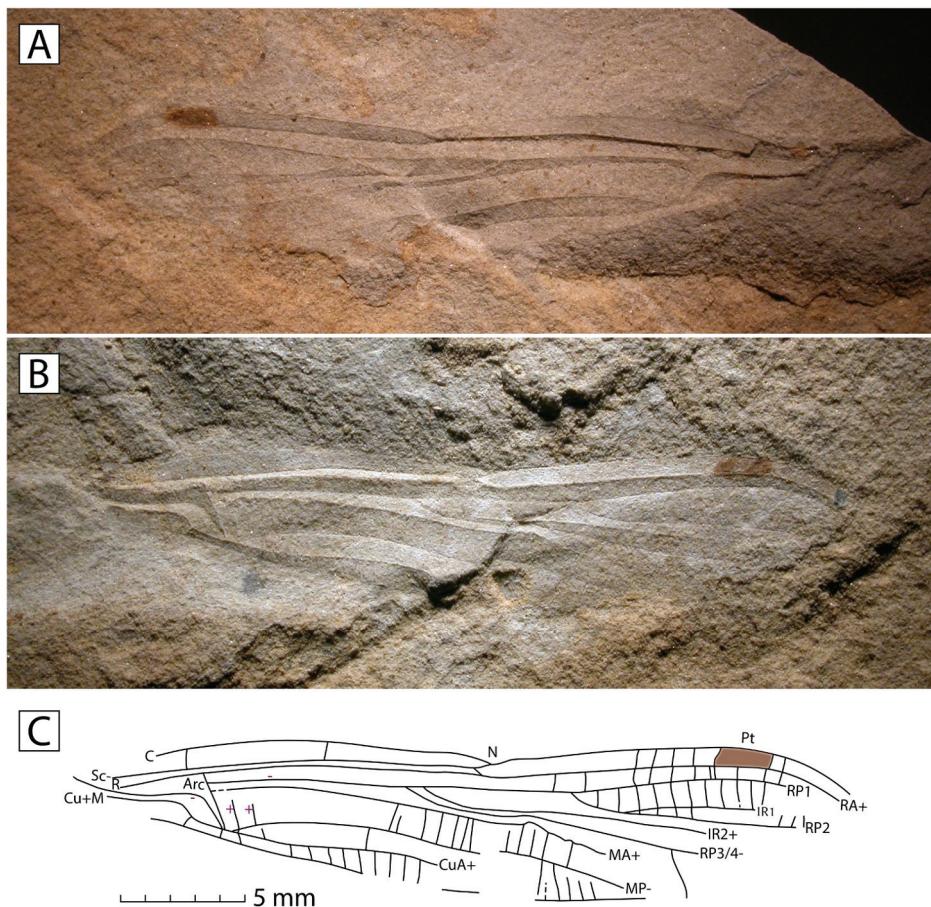


Fig. 5. Print (**B**), counterprint (**A**) and venation drawing (**C**) of forewing of *Italophlebia baueri* sp. n. Holotype, Langenberg outcrop (Lower Saxony, Germany), latest Norian. For abbreviations see above.

Discussion

This fossil forewing is very similar to that of *Italophlebia* from the Rhaetian of Italy (WHALLEY 1986, BECHLY 1997). It shows the synapomorphies of this genus, viz. the distally strongly converging veins RP1 and RP2, and the distally zigzagged vein MA. Nevertheless, it differs from *Italophlebia gervasutti* and *Italophlebia paganoniae* in the shorter pterostigma, covering only two cells, instead of three-four, and the broader subdiscoidal cell of forewing (compared to that of *I. gervasutti*, unknown in *I. paganoniae*). The ratio (wing length/wing width) is 4.79 for *I. gervasutti*, 5.39 for *I. paganoniae*, close to that in *I. baueri* (5.42). Lastly IR1 is nearly completely reduced in *I. paganoniae*, while it is zigzagged in *I. gervasutti*, and nearly straight in *I. baueri*. A further difference with *I. gervasutti* is the more distal nodus near the mid-part of wing.

CONCLUSION

Two new species of the extinct odonate taxa Triassolestoidea, *Triassothemis gartzii* and *Italophlebia baueri*, from the Norian–Rhaetian boundary interval are described. Relatives have been so far reported from Argentina (*Triassothemis mendozensis*, CARPENTER 1960), South Africa (*Afrotriassothemis heidiae* and *Afrotriassothemis regularis*, RIEK 1976) and Italy (*Italophlebia gervasutti* and *Italophlebia paganoniae*, WHALLEY 1986). The occurrence of these taxa in the southern and northern hemisphere of the Triassic world suggests a global dispersal. *Italophlebia baueri* is the first record of this genus outside Italy.

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