

Stuttgarter Beiträge zur Naturkunde

Serie B (Geologie und Paläontologie)

Herausgeber:

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart

| | | | | |
|----------------------------|--------|---------|----------------|-------------------------|
| Stuttgarter Beitr. Naturk. | Ser. B | Nr. 325 | 11 pp., 5 figs | Stuttgart, 31. 12. 2002 |
|----------------------------|--------|---------|----------------|-------------------------|

An interesting new fossil dragonfly (Anisoptera: Libellulidae: “Brachydiplacini”) from the Miocene of Germany, with a discussion on the phylogeny of Tetrathemistinae and a fossil list for the locality Heggbach

By Günter Bechly and Volker J. Sach, Stuttgart

With 5 Figures

Summary

A new dragonfly species, *Parabrachydiplax miocenica* n. gen. n. sp. (Anisoptera: Libellulidae), is described from the early Middle Miocene of Heggbach in southern Germany. The holotype was collected by the priest J. PROBST in 1865 and represents the earliest record of fossil insect remains from the Upper Freshwater Molasse of Baden-Württemberg. The phylogenetic position of this new genus and species is discussed. It is a very primitive Libellulidae of the subfamily Tetrathemistinae, and can be attributed within the latter taxon to a basal grade within the clearly paraphyletic tribus “Brachydiplacini”. The accompanying fauna and flora of *Parabrachydiplax miocenica* n. gen. n. sp. is presented, based on a newly revised fossil list for the locality Heggbach.

Zusammenfassung

Eine neue Libellenart, *Parabrachydiplax miocenica* n. gen. n. sp. (Anisoptera: Libellulidae), wird aus dem unteren Mittel-Miozän von Heggbach in Süddeutschland beschrieben. Der Holotypus wurde schon 1865 von dem Pfarrer J. PROBST gesammelt. Er stellt den ältesten Nachweis von fossilen Insektenresten für die Obere Süßwassermolasse von Baden-Württemberg dar. Die phylogenetische Stellung dieser neuen Gattung und Art wird diskutiert. Es handelt sich um eine sehr ursprüngliche Form der Segellibellen (Libellulidae) aus der Unterfamilie Tetrathemistinae, wo sie in den basalen Bereich des zweifelsfrei paraphyletischen Tribus „Brachydiplacini“ eingeordnet werden kann. Die Begleitfauna und -flora von *Parabrachydiplax miocenica* n. gen. n. sp. wird aufgezeigt anhand einer neu überarbeiteten Fossiliste der Fundstelle Heggbach.

1. Introduction

Today the dragonfly family Libellulidae ranks among the most diverse and widespread subgroups of dragonflies. Surprisingly, there are only few Tertiary dragonfly species described that can be attributed to crown-group Libellulidae. CARPENTER (1992), NEL & PAICHELER (1993) and NEL et al. (1997) reviewed all known taxa of fossil Libellulidae, and BECHLY (1998) discussed the position of the Mesozoic representatives of the libelluloid clade which do not include any crown-group representatives at all. We here describe a new genus and species of dragonfly from the Miocene of Germany that represents the first fossil record of the primitive libellulid tribe "Brachydiplacini" and the earliest record of fossil insect remains from the Upper Freshwater Molasse in Baden-Württemberg.

2. The fossil locality Heggbach

Former sand- and marl-pit at the Buchhaldenberg near the Heggbach mill, about 1 km southwest of the monastery of Heggbach (District of Biberach a. d. Riss, Baden-Württemberg, SW-Germany). Topographic map 1:25000, sheet 7825 Schwendi. – GAUSS-KRÜGER coordinates: R = ³⁵65850, H = ⁵³34500.

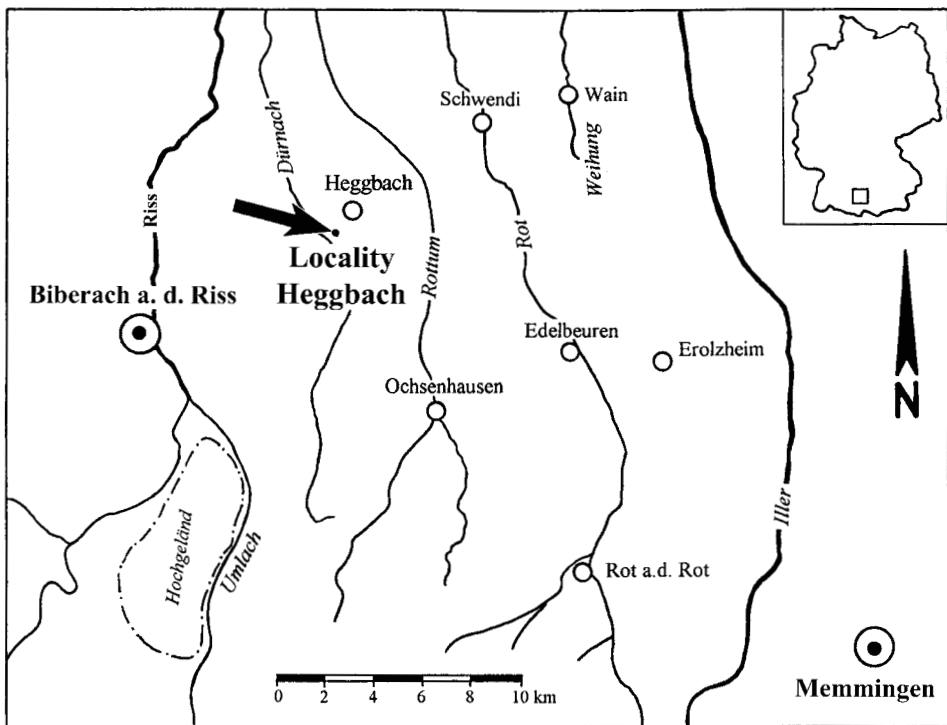


Fig. 1. Geographic map of the fossil locality Heggbach (SW-Germany)



Fig. 2. During the construction of a highway in 1973 the fossiliferous sediments of Heggbach were again exposed. At the base of the dark-coloured coaly horizon, indicated by the arrow, J. PROBST discovered the holotype of *Parabrachydiplax miocenica* n. gen. n. sp. (photo: G. LICHTER, Biberach a. d. Riss).

- Lithology: Argillaceous marl (plant-bearing bed) and layer of coarse-grained reworked rock fragments (vertebrate-bearing layer)
- Topogr. altitude: ~ 545–548 m altitude above sea level
- Lithostratigraphy: Upper Freshwater Molasse (OSM), pre-Riesian
- Age: Early Middle Miocene; mammal unit MN 5 (Orleanian)
- Literature: PROBST (1866, 1868, 1883, 1888); LICHTER & LISKE (1974); GREGOR (1982, 1984); ZÖBELEIN (1983); SACH (1999)

The fossil material is deposited at the Braith-Mali-Museum in Biberach a. d. Riss and the Staatliches Museum für Naturkunde in Stuttgart, Germany.

In the former sand- and marl-pit near Heggbach the priest Dr. J. PROBST (1823–1905) from the area of Biberach discovered fossiliferous layers of the Upper Freshwater Molasse. From the year 1857 onwards he could at first only discover fossil vertebrate remains from an irregular (lenticulated) layer of reworked rock fragments (“Knauerschicht”), mainly bones and teeth of large mammals as well as isolated carapax plates of turtles. Later, in the year 1865, a plant-bearing bed was discovered 2–3 meters below the vertebrate-bearing layer. In the argillaceous marl of this bed PROBST discovered several thousand fossil plant remains (impressions of leaves, fructifications, and seeds). In lesser amount gastropod shells, fish remains and impressions of insects have been found, including the here described dragonfly wing. Some further insect remains from the same locality are still present in the collection PROBST, viz. some Coleoptera elytrae and a fragment of insect mouth parts (resembling the mask of a large dragonfly larva).

List of known fossil taxa from Heggbach

Plantae*:

Limnocarpus eseri GREGOR
Gleditsia knorrii GREGOR
Alnus kefersteinii UNGER
Alnus julianaeformis KVAČEK & HOLY
Populus mutabilis HEER
Populus balsamoides GOEPPERT
Populus sp.
Ulmus braunii HEER
Zelkova ungeri (ETTINGSHAUSEN) KOV.
Sapindus falcifolius (A. BRAUN)
Berchemia sp.
Daphnogene polymorpha ETTINGSHAUSEN
Daphnogene sp. (type "lanceolata" HEER)
 cf. *Taxus* sp.
 div. gen. et sp. (u. a. *Carex*, *Phragmites*,
Equisetum, *Betula*, *Acer*, *Celtis*; s. PROBST
 1879)

Gastropoda:

Coretus cf. *cornu* (BRONGNIART)
Lymnaea dilatata NOULET
Brotia escheri (BRONGNIART)
Cepaea silvana (KLEIN)
Tropidomphalus aff. *zellii* (KURR)

Bivalvia:

Unio sp.

Insecta:

Parabrachydiplax miocenica nov. gen. et sp.
 Coleoptera div. indet.
 Mouthparts of an unknown insect (mask of
 dragonfly larva?)

Actinopterygii:
 Teleostei div. indet.

Lepidosauria – Squamata:
Ophisaurus sp.; s. PROBST (1879: 261)

Chelonia:
Trionyx sp.
Ocadia sp.
Testudo sp.
Geochelone sp.
 Crocodylia:
Diplocynodon sp. **

Aves:
 indet.; bone remains

Mammalia:
Steneofiber depereti MAYET
Prolagus oeningensis (KÖNIG); s. SCHLOSSER
 (1904: 487)
Amphicyon major BLAINVILLE
 Amphicyonidae indet. (cf. *Cynelos* sp.)
Anchitherium aurelianense aurelianense
 ABUSCH-SIEVERT
Plesiaceratherium fablbuschi (HEISSIG)
Prosantorhinus germanicus (WANG)
Hyotherium soemmeringi H. v. MEYER
Lagomeryx ruetimeyeri THENIUS
Procervulus dichotomus (GERVAIS)
 Cervidae indet. (size like *Euprox/Hetero-*
prox sp.)
Palaeomeryx kaupi H. v. MEYER
Dorcatherium nauii KAUP
Gomphotherium angustidens (CUVIER)

*) Comment: For the plants, only the more recent determinations by GREGOR (1982, 1984) and our own determinations are referred to. Numerous further plant taxa determined by O. HEER can be found in the publications of PROBST (1868, 1879, 1883, 1884).

**) Comment: The crocodile genus *Diplocynodon* POMEL, 1847 should not be confused with the Upper Jurassic mammal-like "reptile" *Diplocynodon* MARSH, 1880 which is an invalid junior homonym and a senior synonym of *Docodon* MARSH, 1881. Because of the homonymy *Docodon* has to be considered as the next available valid genus name for this latter taxon.

The fossil locality Heggbach can be clearly attributed to the pre-Riesian part of the Upper Freshwater Molasse because of its topographic altitude and its geographical position relative to the outcrops of the "Brockhorizont" near Biberach (base at 603.5 m altitude above sea level) (SACH, 1997, 1999). Furthermore, in a supplement-volume of the Württembergische Jahrbücher (Höhenbestimmungen und Notizen für das Atlasblatt Laupheim; REGELMANN et al., 1877: 96, 102) altitude data are provided for the occurrence of the "Albstein" (boundary horizon between the Upper Marine Molasse and the Upper Freshwater Molasse) northeast of Biberach: about

536 m altitude above sea level at Walpertschhofen and about 543 m altitude above sea level at Heggbach. Sediments of the Upper Marine Molasse, the so-called Baltringer Schichten (Baltringen Beds) are exposed in the vicinity of the “Albstein” outcrops. Consequently, the base of the Upper Freshwater Molasse must be situated in a short vertical distance below the locality Heggbach.

The co-occurrence of the cervoids *Lagomeryx ruetimeyeri* and *Procerovulus dichotomus* as well as the rhinocerotids *Plesiaceratherium fahlbuschi* and *Prosantorhinus germanicus* strongly suggests an attribution of the Heggbach beds to the unit MN 5 of mammal biostratigraphy. This is consistent with the relatively low evolutionary level of the proboscidian *Gomphotherium angustidens*.

Today the outcrops of the fossil-bearing outcrops of Heggbach are filled up and overgrown. More recently the fossiliferous layers were again exposed during the construction of a new highway (see Fig.2) in 1973, where further fossil plants and gastropods could be collected (LICHTER & LISKE, 1974).

| EPOCH | PARATETHYAN STAGES | MAMMAL STRATIGRAPHY | | LITHOSTRATIGRAPHY, NW-part of Molasse Basin | |
|-------------------------|---------------------|---|--|---|---|
| | | Mammal-Units | Sites in SW-Germany | | |
| Middle Miocene | Sarmatian 13,0 | Astaracian | MN 7+8 | Steinheim a. Albuch | Hiatus |
| | Badenian 15,0 Ma | | MN 6 | Steinberg/Ries | |
| | 16,4 | O r l e a n i a n | MN 5/6 | Wannenwaldtobel 2 Edelbeuren-Maurerkopf | Brockhorizont post-Riesian OSM * RIES IMPACT |
| | | | MN 5 | Heggbach Engelswies | pre-Riesian O S M |
| Karpatian 17,2 | MN 4/5 | | Gerlenhofen | BM/OSM (transitional facies) | |
| | Ottungian 18,0 | | 4b | Langenau 1 | B M Kirchberger Schichten Suevicus Schichten Grimmfinger Schichten |
| MN 4 | | Illerkirchberg 1 Eggingen-Mittelhart 3 | | | |
| 4a | | Baltringen | | | |
| Eggenburgian 20,5 | Agenian | MN 3 | Stubersheim 3 | OMM Hiatus | |
| Egerian | | MN 2 | Ulm-Westtangente | U S M | |
| | | MN 1 | Altheim-Breitenlauch 1 | | |
| Upper Oligo. 25,0 Ma | Arvernian | MP 30 | Eggingen-Erdbeerhecke Eggingen-Mittelhart 1+2 | | |

Fig. 3. Stratigraphic correlation of the Paratethyan Stages and the Mammal Units with the lithostratigraphic succession at the northwestern part of the Molasse Basin (SW-Germany) including the locality Heggbach. USM = Lower Freshwater Molasse; OMM = Upper Marine Molasse; BM = Brackish Water Molasse; OSM = Upper Freshwater Molasse. The “Albstein” is not shown in this figure, but is a thin terrestrial equivalent of the Brackish Water Molasse.

3. Methods

The drawing was made with a camera lucida on a Wild M5 binocular microscope, and the photo was made by directly scanning the fossil with a flatbed scanner. The nomenclature of the dragonfly wing venation is based on the interpretations of RIEK & KUKALOVÁ-PECK (1984), amended by NEL et al. (1993) and BECHLY (1996).

4. Systematic Palaeontology

Class Insecta LINNAEUS, 1758 (= Hexapoda LATREILLE, 1825)

Pterygota BRAUER, 1885

Order Odonata FABRICIUS, 1793

Suborder Anisoptera SELYS in SELYS & HAGEN, 1854

Cavilabiata BECHLY, 1996

Family Libellulidae LEACH, 1815

Subfamily Tetrathemistinae TILLYARD, 1917

Tribus "Brachydiplacini" TILLYARD, 1917

Genus *Parabrachydiplax* n. gen.

Type species: *Parabrachydiplax miocenica* n. sp., by present designation.

Derivation of name: Named after the similarity with the extant genus *Brachydiplax*.

Diagnosis. – Same as type species since monotypic.

Parabrachydiplax miocenica n. sp.

Figs 3–4

Holotype: Specimen no. P569 at the Braith-Mali-Museum in Biberach a. d. Riss, Germany. It is a plate and counterplate of an isolated fragment of a wing and the only known specimen of this new genus and species.

Type locality: Former sand- and marl pit at Heggbach, district of Biberach a. d. Riss, Baden-Württemberg, SW-Germany.

Type horizon: Early Middle Miocene, Upper Freshwater Molasse (OSM), mammal unit MN 5

Derivation of name: Named after the Miocene age of this fossil.

Diagnosis. – This new libellulid species can be distinguished by the following combination of characters: Most distal antenodal of the first row incomplete and oblique; antenodals mostly aligned, primary antenodals not distinguishable; 6 postnodal and 3 postsubnodal crossveins; long "libellulid gap"; two crossveins beneath pterostigma, including the slightly displaced stigmal brace vein; pseudo-IR1 originates beneath basal third of pterostigma; basal unicellular area between RP1 and RP2 only 4 cells long; third crossvein between RP1 and RP2 distinctly oblique ("libellulid oblique vein"); apical supplement sector present between RP1 and RP2; R_{spl} straight and parallel to IR2, ending on the posterior wing margin; only one row of cells between R_{spl} and IR2.

Description

An isolated fragment of the costal area and the distal half of a dragonfly forewing of unknown sex. The wing venation is very well-preserved, but the wing base with important characters such as arculus and triangle is missing.

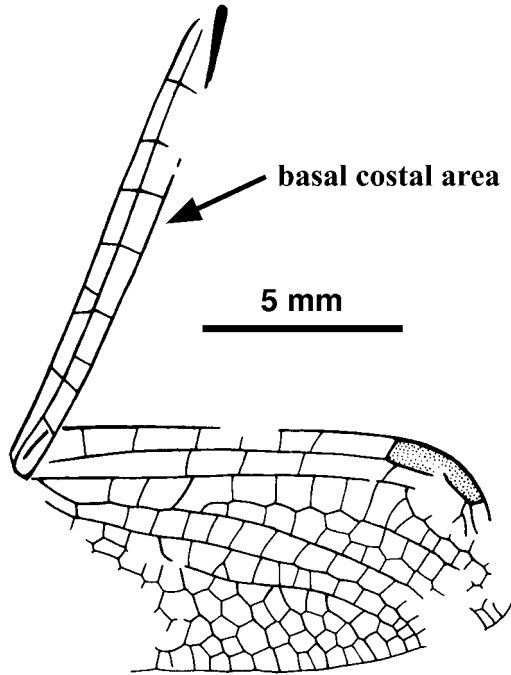


Fig. 4. *Parabrachydiplax miocenica* n. gen. n. sp., holotype P569, forewing (the costal area basal of the nodus is displaced upwards). Scale 5 mm.

Wing: Length of wing 25.4 mm; width of distal half of wing 6.3 mm; distance between wing base and nodus 13.1 mm; distance between nodus and pterostigma 9.2 mm. Position of nodus at 52 % of wing length, thus it must be a forewing. Pterostigma 2.7 mm long and max. 0.8 mm wide; there are two postsubnodal crossveins beneath the pterostigma, the basal one being an oblique stigmal brace vein that is shifted 0.4 mm distal of the anterior side of the pterostigma. 8 antenodal crossveins between C and ScP and 7 between ScP and RA; 6 of the antenodals are well-aligned; the most distal antenodal in the first row is incomplete; the primary antenodals Ax1 and Ax2 are not distinguishable from the secondaries. 6 postnodal crossveins between nodus and pterostigma, not aligned with the 3 corresponding postsubnodal crossveins basal of the pterostigma. There is a distinct and long gap of postsubnodal crossveins ("libellulid gap") directly distal of the subnodus. Base of RP2 probably aligned with subnodus. One oblique vein 'O', one cell and 1.2 mm distal of the subnodus (estimated by the origin of RP2). A strong Rspl which is straight and parallel to IR2 and reaches the posterior wing margin; only one row of cells between IR2 and Rspl; Rspl originates 3.5 mm distal of the origin of RP2; several convex secondary longitudinal veins originate on Rspl and reach the posterior wing margin. IR2 and RP2 are parallel and straight with only a single row of cells in-between. RP1 and RP2 are strongly divergent, so that basal unicellular area in-between is only 4 cells long; the third crossvein between RP1 and RP2 is distinctly oblique and most probably represents a "libellulid oblique vein" that is shifted one cell distad in the course of beginning reduction (as in the related extant libellulid



Fig. 5. *Parabrachydiplax miocenica* n. gen. n. sp., holotype P569, wing. Scale as indicated by the ruler.

genus *Thermochoria*). A pseudo-IR1 originates on RP1 beneath the basal third of the pterostigma. A convex apical supplement sector is present but relatively weakly developed. Three rows of cells between pseudo-IR1 and RP2.

5. Phylogenetic considerations

Within Anisoptera *Parabrachydiplax* n. gen. shares several synapomorphies with the taxa Cristotibiata (pterostigmata not parallel-sided, distal side more oblique than basal side, and rather stout with length less than 8 times width), Brachystigmata (wings with relatively short pterostigmata that cover only 1–3 complete cells), Pan-eurypalpidomorpha (lestine oblique vein only 1–2 cells distad of the subnodus in

both pairs of wings), Eurypalpidiformia (pterostigma further shortened, only 1–2 cells long), Paneuryalpida (basal part of postsubnodal area free of crossveins, “libellulid gap”), Euryalpida (pterostigmal brace vein shifted distally beneath the pterostigma; area between RP2 and IR2 not distinctly widened distally), Neolamellicida (nearly all antenodal crossveins are aligned; the two primary antenodal brackets Ax1 and Ax2 are at least somewhat less distinct), Mediocostida (presence of a distinct Rspl that is more or less parallel to IR2 in the groundplan) and Libellulida (presence of a putative vestige of the “libellulid oblique vein”; the area between RA and RP1 stays only unicellular for 2–5 cells, because RA and RP1 are distinctly diverging).

It can be excluded from crown-group Corduliidae s.str. because of the plesiomorphic presence of two crossveins beneath the pterostigma, compared to only one crossvein (displaced stigmal brace) in Corduliidae sensu BECHLY (1996). It also lacks the autapomorphies of crown-group Urothemistidae (= Macrodiplacidae), but shares some synapomorphies with Libellulidae (= Eulibellulida sensu BECHLY, 1996) (the two primary antenodal brackets Ax1 and Ax2 are indistinguishable from the secondaries; a concave apical supplement sector developed between RP1 and RP2; vein pseudo-IR1 originates beneath the basal part of the pterostigma; the most distal antenodal between costal margin and ScP is developed as an antenodal oblique vein, while the corresponding antenodal between ScP and RA is secondarily absent).

It does not share any visible synapomorphies with one of the libellulid subfamilies, except for Tetrathemistinae sensu BECHLY (1996). With the latter subfamily this new fossil taxon shares a Rspl that is secondarily more or less parallel to IR2, and a more or less reduced “libellulid oblique vein”. The fact that Urothemistidae show the derived condition (curved Rspl that ends on IR2, very distinct “libellulid oblique vein”) clearly demonstrates that these character states are shared apomorphic reversals and not shared plesiomorphies.

Within Tetrathemistinae the new taxon falls into the paraphyletic tribe “Brachydiplacini”. The latter group was originally classified as separate subfamily of Libellulidae, but BECHLY (1996) classified the original subfamilies Brachydiplacinae and Tetrathemistinae as tribes within a monophyletic subfamily Tetrathemistinae sensu BECHLY (1996). All Tetrathemistinae share a set of highly derived characters, such as the complete reduction of the “libellulid oblique vein”, a Rspl that is secondarily straight and reaching the wing margin, a strange quadrangular discoidal triangle in the forewings or in both pairs of wings, and a strongly reduced cubito-anal area in the hindwings which can even imply the complete reduction of the anal loop in some derived genera (e.g. *Eothemis*, *Palaeothemis*, and *Risiophlebia*) that rather look like zygopteres.

In Brachydiplacini there are genera (e.g. *Anatya*, *Argyrothemis*, *Eleuthemis*, *Fylgia*, *Nannophya*, *Nannophyopsis*, *Nannothemis*, and *Nephepeltia*) that share at least some of these characters with Tetrathemistinae, while there are other genera (e.g. *Brachydiplax*, *Chalybeothemis*, *Edonis*, *Micrathyria*, *Hemistigma*, *Thermochoria*, and *Porpacithemis*) that are still closer to the groundplan of Libellulidae and exhibit the concerning plesiomorphic states (large cubito-anal area, triangular discoidal triangles, distinct “libellulid oblique vein”). This pattern of character distribution within “Brachydiplacini” clearly demonstrates that this tribe has to be regarded as highly paraphyletic assemblage, that represents a grade towards Tetrathemistini.

Within this grade *Parabrachydiplax* n. gen. most closely resembles more basal genera like *Brachydiplax* and *Thermochoria* (because of the retention of the “libellulid oblique vein”), but not the most basal genera like *Chalybeothemis*, *Hemistigma* and *Micrathyria* which still have a curved Rspl that ends on IR2 (groundplan character of Anauriculida = Hemicorduliidae, Urothemistidae and Libellulidae).

6. Acknowledgements

We are indebted to Mr F. BRUNCKER (Biberach), director of the Braith-Mali-Museum, for a loan of the fossil insect remains from Heggbach. We thank Mr G. LICHTER (Biberach) for supplying a photo of the outcrop in Heggbach. We are most grateful to Dr G. BLOOS (SMNS, Stuttgart) for his careful proof-reading of this manuscript.

7. References

- BECHLY, G. (1996): Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der *Odonata. – *Petalura*, spec. vol. 2: 1–402; Böblingen.
- (1998): *Juracordulia schiemenzi* gen. et. sp. nov. Eine neue Libelle aus den Solnhofener Plattenkalken (Insecta: Odonata: Anisoptera). – *Archaeopteryx*, 16: 29–36; Munich.
- CARPENTER, F. M. (1992): Superclass Hexapoda. – *In*: MOORE, R. C. & KAESLER, R. L. (eds.): *Treatise on Invertebrate Paleontology*. (R), Arthropoda 4, 3–4. – xxii + 655 pp.; Boulder (Geological Society of America) and Lawrence (University of Kansas).
- GREGOR, H.-J. (1982): Die jungtertiären Floren Süddeutschlands – Paläokarpologie, Phytostatigraphie, Paläoökologie, Paläoklimatologie. 278 pp., 34 figs, 16 pls, Anhang; Stuttgart (Enke).
- (1984): Die jungtertiäre Florenabfolge der westlichen Vorland-Molasse (Günzburg-Biberach a. d. Riß) und die paläofloristische Bestätigung der DEHM'schen Serien. – *In*: August-Wetzler-Gedenkband – Molasseforschung ,84. – Heimatliche Schriftenreihe für den Landkreis Günzburg, Bd. 2: 79–86, 1 fig., 4 tabs; Günzburg (Histor. Ver. Günzburg).
- LICHTER, G. & LISKE, T. (1974): Heggbach, eine vergessene Fundstelle der Oberen Süßwassermolasse. – *Der Aufschluß*, 25/6: 308–312, 6 figs, 1 tab.; Heidelberg.
- NEL, A., MARTÍNEZ-DELCLÒS, X., PAICHELER, J.-C. & HENROTAY, M. (1993): Les “Anisozygoptera” fossiles. Phylogénie et classification. (Odonata). – *Martinia*, Numéro hors-série, 3: 1–311; Bois-d'Arcy.
- NEL, A., MARTÍNEZ-DELCLÒS, X., PAPIER, F. & OUDARD, J. (1997): New Tertiary Odonata from France (Sieblosiidae, Lestidae, Coenagrionidae, Megapodagrionidae, Libellulidae). – *Dtsch. ent. Z.*, 44/2: 231–258; Berlin.
- NEL, A. & PAICHELER, J.-C. (1993): Les Libellulidae fossiles. Un inventaire critique. – *Ent. gallica*, 4/4: 166–190; Avon.
- PROBST, J. (1866): Geognostische Skizze der Umgebung von Biberach. – *Jh. Ver. vaterl. Naturk. Württ.*, 22: 45–60; Stuttgart.
- (1868): Tertiäre Pflanzen von Heggbach bei Biberach nebst Nachweis der Lagerungsverhältnisse. – *Jh. Ver. vaterl. Naturk. Württ.*, 24: 172–185; Stuttgart.
- (1879): Verzeichnis der Fauna und Flora der Molasse im Württembergischen Oberschwaben. – *Jh. Ver. vaterl. Naturk. Württ.*, 35: 221–304, 2 pls; Stuttgart.
- (1883): Beschreibung der fossilen Pflanzenreste aus der Molasse von Heggbach OA. Biberach und einigen andern oberschwäbischen Localitäten. Erste Abtheilung: Dicotyledonen. – *Jh. Ver. vaterl. Naturk. Württ.*, 39: 166–242, 2 pls; Stuttgart.
- (1884): Beschreibung der fossilen Pflanzenreste aus der Molasse von Heggbach OA. Biberach und einigen andern Localitäten. Zweite Abtheilung: Monocotyledonen, Gymnospermen, Cryptogamen. – *Jh. Ver. vaterl. Naturk. Württ.*, 40: 65–95, 1 pl.; Stuttgart.

- (1888): Beschreibung einiger Lokalitäten in der Molasse von Oberschwaben. Vorträge. – Jh. Ver. vaterl. Naturk. Württ., **44**: 64–114; Stuttgart.
- REGELMANN, C. & GROSS, H. (1877): Trigonometrische Höhenbestimmungen und Notizen über den Gebirgsbau für die Atlasblätter Ehingen, Laupheim und Riedlingen. – Württ. Jb. Statistik u. Landesk., Suppl.-Bd. (1877): 63–139; Stuttgart.
- RIEK, E. F. & KUKALOVÁ-PECK, J. (1984): A new interpretation of dragonfly wing venation based upon early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. – Can. J. Zool., **62**: 1150–1166; Ottawa.
- SACH, V. J. (1997): Neue Vorkommen von Brockhorizonten in der Oberen Süßwassermolasse von Baden-Württemberg (Deutschland) – Zeugnisse der Rieskatastrophe im Mittelmiozän. – N. Jb. Geol. Paläont. Abh., **205/3**: 323–337, 8 figs; Stuttgart.
- (1999): Litho- und biostratigraphische Untersuchungen in der Oberen Süßwassermolasse des Landkreises Biberach a. d. Riß (Oberschwaben). – Stuttgarter Beitr. Naturk., B, **276**, 167 pp., 41 figs, 45 tabs, 15 pls; Stuttgart.
- SCHLOSSER, M. (1904): Notizen über einige Säugethierfaunen aus dem Miocän von Württemberg und Bayern. – N. Jb. Min. Geol. Paläont., Beil.-Bd., **19**: 485–502, 1 pl.; Stuttgart.
- ZÖBELEIN, H. K. (1983): Die Vorlandmolasse bei Günzburg a. d. Donau und Heggbach bei Biberach a. d. Riß im Rahmen des süddeutschen Jungtertiärs. – Mitt. Bayer. Staatssl. Geol. hist. Geol., **23**: 151–187, 2 tabs; München.

Addresses of the authors:

Dr G. Bechly, Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, Germany.

E-mail: bechly.smns@naturkundemuseum-bw.de

Dr V. J. Sach, In der Werre 23, D-70619 Stuttgart, Germany.

E-mail: vsach@gmx.de

ISSN 0341-0153

Schriftleitung: Dr. Gert Bloos, Rosenstein 1, D-70191 Stuttgart
Gesamtherstellung: Gulde-Druck GmbH, D-72072 Tübingen