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A re-description of "*Stenophlebia*" *casta* (Insecta: Odonata: Parastenophlebiidae n. fam.) from the Upper Jurassic Solnhofen Limestone in Germany

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Abstract

The enigmatic fossil dragonfly "*Stenophlebia*" *casta* from the Upper Jurassic Solnhofen Limestone in Germany is re-described and its wing venation figured for the first time, based on several new specimens, including a very well-preserved specimen with perfect wing venation. Previously this taxon had to be considered as a nomen dubium within Odonata incertae sedis, because the holotype is lost and the original description is insufficient. Now, its previous attribution to the genus *Stenophlebia* and the family Stenophlebiidae can be clearly rejected. The species is here attributed to a new family (Parastenophlebiidae n. fam.) and genus (*Parastenophlebia* n. gen.) of Heterophlebioptera – Heterophlebioidea, representing a basal branch close to Liassophlebiidae.
Keywords: Odonata, "Anisozygoptera", Heterophlebioidea, Stenophlebiidae, *Stenophlebia*, dragonfly, fossil, Jurassic, Lithographic Limestone, Solnhofen, Bavaria.

Zusammenfassung

Die rätselhafte fossile Libelle „*Stenophlebia*" *casta* aus dem oberjurassischen Solnhofener Plattenkalk in Deutschland wird auf der Grundlage von mehreren neuen Exemplaren, von denen eines besonders gut mit perfektem Flügelgeäder erhalten ist, wiederbeschrieben und erstmals das Flügelgeäder abgebildet. Zuvor musste dieses Taxon als Nomen dubium in Odonata incertae sedis angesehen werden, da der Holotypus verschwunden und die Originalbeschreibung unzureichend ist. Jetzt kann die bisherige Zuordnung zu der Gattung *Stenophlebia* und der Familie Stenophlebiidae eindeutig widerlegt werden. Die Art wird hier einer neuen Familie (Parastenophlebiidae n. fam.) und Gattung (*Parastenophlebia* n. gen.) der Heterophlebioptera – Heterophlebioidea zugeordnet, und zwar als basaler Seitenzweig nahe der Liassophlebiidae.

1. Introduction

Heterophlebia casta Hagen, 1862 was only very briefly described without any figure. The original description only states that the type is a male dragonfly from

Eichstätt with a body length of 55 mm and a wing span of 64 mm. Later, HANDLIRSCH (1906: 582) provided a precise wing length of 31 mm, mentioned the presence of a perpendicular triangle and a clubbed apex of the abdomen with short cerci. Obviously based on these similarities with Stenophlebiidae, and probably the very similar oblique position of the wings, he transferred the species to the genus *Stenophlebia*, and even remarked that he is very confident that this attribution is justified. *Stenophlebia casta* was subsequently not discussed in the literature before NEL et al. (1993: 125), who indicated that they could not find the holotype in the museum of Munich, and transferred the taxon to "*Stenophlebia* (?) sp. incertae sedis". The latter decision is taxonomically invalid because a described species cannot be attributed to "sp. incertae sedis". The intention of the authors obviously was to indicate that *Stenophlebia casta* is a doubtful taxon, and therefore they should rather have regarded it as a nomen dubium. Within the last years the author of the present work could discover several putative specimens of this species in various private and official collections. However, until recently, none of these specimens showed more than the general habitus, and therefore were unsuited for a re-description of this taxon. Such a re-description is now made possible by a new specimen that is very well preserved, including the most important wing venation. Finally, after more than 140 years, it is now possible to provide a detailed description and diagnosis as well as figures of this enigmatic dragonfly taxon from the Solnhofen limestones, and to analyse its position in the phylogenetic system of dragonflies. The attribution of all these specimens to the same species "*Stenophlebia*" *casta* is founded on the corresponding size, the common stenophlebiid-like habitus including a transverse discoidal cell, oblique position of the wings, and the extremely clubbed apex of the abdomen. This specific attribution can be regarded as very well supported indeed, because such a combination of characters is not present in any other fossil odonate from the Solnhofen limestones. The present re-description clearly shows that "*Stenophlebia*" *casta* does neither belong to the genus *Stenophlebia* nor to the family Stenophlebiidae. It is identified as a member of Heterophlebioptera – Heterophlebioidea and attributed to a new family (Parastenophlebiidae n. fam.) and genus (*Parastenophlebia* n. gen.) which seems to be rather close to Liassophlebiidae.

Abbreviations

BMMS Bürgermeister-Müller-Museum in Solnhofen
JME Jura Museum Eichstätt
SMNS Staatliches Museum für Naturkunde Stuttgart

Acknowledgements

I am most grateful to Mr P. BÜRGER (Bad Hersfeld) for the kind loan of the wonderful specimen of *Parastenophlebia casta* n. comb. and for his decision to make a will to donate this specimen to a public museum. I thank Dr G. RÖPER (Bürgermeister-Müller-Museum, Solnhofen), Dr G. VIOHL (Jura Museum, Eichstätt), and Mr G. STÖBENER (Staufenberg) for the loan of further specimens of this taxon. I am indebted the late Mr K. A. FRICKHINGER (Emmering), to whom I dedicate this publication, for providing a lot of information and numerous photos of fossil odonates from Solnhofen. I am grateful to Mr G. KOSCHNY (Bad Soden-Salmünster) for providing a photo of his specimen. Finally, I thank Dr R. BÖTTCHER (SMNS, Stuttgart) and the two referees (Dr A. NEL, MNHN, Paris; and Prof. Dr C. BRAUCKMANN, TU Clausthal) for their careful proof-reading of this manuscript and useful comments.

2. Methods

The drawings were made with a camera lucida and a binocular microscope. Most photos are macro photos made with a SLR camera, but the "photo" of the type specimen (Fig. 5) was made by the author by directly scanning the fossil with a flatbed scanner with a resolution of 1200 dpi. 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), and the phylogenetic classification of Odonata is based on BECHLY (1996, 2002). The systematic analysis is based on the principles of consequent Phylogenetic Systematics (sensu HENNIG 1966, 1969, and BECHLY 2000).

3. Systematic Palaeontology

Class Insecta LINNAEUS, 1758 (= Hexapoda LATREILLE, 1825)
Pterygota BRAUER, 1885
Order Odonata FABRICIUS, 1793
Epiproctophora BECHLY, 1996
Euepiproctophora BECHLY, 1998
Anisopteromorpha BECHLY, 1996
Suborder Heterophlebioptera BECHLY, 1996
Heterophlebioidea NEEDHAM, 1903

Family Parastenophlebiidae n. fam.

Type genus: *Parastenophlebia* n. gen., by present designation.

Diagnosis. – See diagnosis of type genus, since monotypic.

Autapomorphies: all secondary antenodal crossveins of both rows secondarily absent; vein IR1 completely suppressed; vein pseudo-IR1 well-developed, parallel to RP1, and originating beneath the middle of the pterostigma; very strongly thickened margins of pterostigma; size of cubito-anal area of hind wing secondarily reduced.

Genus *Parastenophlebia* n. gen.

Type species: *Parastenophlebia casta* (HAGEN, 1862) n. comb., by present designation.

Derivatio nominis: After the superficial similarity to the habitus of the fossil dragonfly genus *Stenophlebia* and the previous incorrect attribution to this genus.

Diagnosis. – See diagnosis of type species, since monotypic. Autapomorphies therefore same as family.

Parastenophlebia casta (HAGEN, 1862) n. comb.
Figs 1–9

1862 *Heterophlebia casta*. – HAGEN, p. 106.
1869 *Heterophlebia casta* HAGEN. – WEYENBERGH, p. 235. [Incorrectly synonymized with *Libellula brevialata* MÜNSTER, 1839 which is a nomen nudum according to FLECK et al. 2003]

1906 *Stenophlebia casta* HAGEN. – HANDLIRSCH in HANDLIRSCH 1906–1908, p. 582. [Considered attribution to genus *Stenophlebia* as well founded]
1993 *Stenophlebia casta* (HAGEN, 1862). – NEL et al., p. 125. [Transferred to *Stenophlebia* (?) sp. incertae sedis n. stat.]
1999 *Stenophlebia casta* (HAGEN, 1862). – FRICKHINGER, p. 56, fig. 96.
2003 ?*Stenophlebia casta* (HAGEN, 1862). – FLECK et al., p. 85, figs 38–39.

Holotype: The holotype should be in the Bayerische Staatsammlung für Geologie und Paläontologie in Munich, but unfortunately it has to be regarded as lost according to NEL et al. (1993: 125), FLECK et al. (2003), and my own investigations. Probably it was destroyed during the Second World War. FLECK et al. (2003) therefore designated specimen SOS 4656 from the Jura Museum in Eichstätt as neotype.

Type locality: Eichstätt, southern Frankonian Alb, Bavaria, Germany.

Type horizon: Solnhofen Lithographic Limestone, Solnhofen Formation (Malm zeta 2b, "oberer Weißjura"), Hybonotum Zone, Upper Jurassic, Lower Tithonian.

New material: The present re-description is mainly based on the perfectly preserved specimen from the private coll. BÜRGER (Bad Hersfeld) (Figs 1–5). The neotype specimen no. SOS 4656 (ex coll. SCHÄFER) in the Jura Museum in Eichstätt (Fig. 6) was figured by FLECK et al. (2003: 85, fig. 38). The specimen no. BMMS 266a and b (old numbers 319 and 320) in the Bürgermeister-Müller-Museum in Solnhofen was already figured by FLECK et al. (2003, fig. 39) as well. A further specimen no. MA 237a and b is in private coll. STÖBENER (Staufenberg) (Figs 7–8). And a specimen with number 0013 is in private coll. KOSCHNY (Bad Soden-Salmünster) (Fig. 9), of which the counter plate is in private coll. KÜMPEL (Wuppertal). Finally, there shall be three specimens in private coll. KNODEL (Ilze), of which a very well preserved specimen (however with wings superimposed) was figured by FRICKHINGER (1999: 56–57, fig. 96). The alleged specimen of *"Stenophlebia" casta* figured in FRICKHINGER (1994: 140, fig. 260) is actually a *Tarsophlebia eximia* (FRICKHINGER 1999: 56).

New diagnosis. – Body length about 44–48 mm; wing length about 27–31 mm; all main veins (except CuA) are very long and end distinctly distal of the nodus (MP and MA) or even distal of the pterostigma (RP3/4, IR2, RP2); cells between the main longitudinal veins are transversely elongated; all secondary antenodal crossveins of both rows secondarily absent; forewing discoidal cell narrow, acute, and basally open, without a division into hypertriangle and triangle; hind wing discoidal cell basally closed by a curved crossvein, but also not divided into hypertriangle and triangle; RP2 not aligned with subnodus, but originating far distal of it; vein IR1 completely suppressed; vein pseudo-IR1 well-developed, parallel to RP1, and originating beneath the middle of the pterostigma; numerous (about 10) postnodal crossveins; very strongly thickened margins of pterostigma; vein CuA with numerous branches; size of cubito-anal area of hind wing secondarily reduced.

Description. – Specimen in coll. BÜRGER (Figs 1–5)

A completely preserved dragonfly of unknown sex. The wing venation is partly traced by iron oxide dendrites.

Body: Total body length 48 mm; width of head 5.5 mm (eyes well separated); length of abdomen 33 mm; width of abdomen min. 1.5 mm and max. 5.0 mm at the distinct apical expansion; the femora of three folded legs are visible as well but do not show any details. The wings are preserved in typical "anisozygopterid" position obliquely directed backwards.

Forewing: Preserved length 29.5 mm (estimated total length about 30.5 mm); width at nodus 6.0 mm; distance from base to nodus 13.7 mm (the nodus is situated at about 45 % of the estimated wing length, thus in a very basal position compared to true Anisoptera forewings); distance from nodus to pterostigma 10.9 mm; Ax1 is not preserved, Ax2 is at least not clearly preserved either; apparently there were no

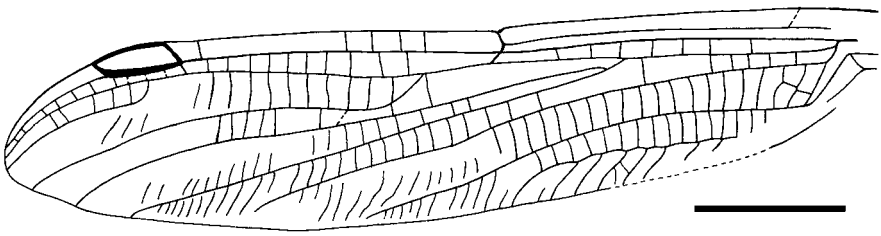

Fig. 1. *Parastenophlebia casta* n. comb., right forewing from below; coll. BÜRGER, without number. – Scale bar: 5 mm.

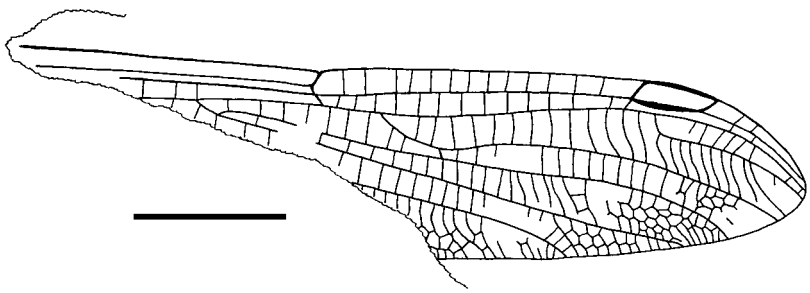

Fig. 2. *Parastenophlebia casta* n. comb., left forewing from below; coll. BÜRGER, without number. – Scale bar: 5 mm.

secondary antenodal crossveins; numerous (at least 7) antesubnodal crossveins in the middle of the antesubnodal area; 13 postnodal crossveins between nodus and pterostigma, non-aligned with the corresponding 13 postsubnodal crossveins; no "libelluloid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 2.5 mm long and max. 1.0 mm wide; its distal side is much more oblique than its basal side; the margins of pterostigma are very strongly thickened; the pterostigma is distinctly braced and might cover several cells (indistinctly preserved); the arculus is incomplete, because the discoidal cell is basally open; bases of veins RP and MA (sectors of arculus) widely separated at the arculus; the discoidal cell is long (2.3 mm) and narrow (0.4 mm), and not divided into hypertriangle and triangle; MAb is 1.6 mm long and straight; a short (0.7 mm) but distinct pseudo-anal vein PsA (= AA0) delimits a long, narrow, and unicellular subdiscoidal triangle; basal space free; cubital cell free; CuP-crossing not preserved; anal area reduced (apparently the wing was shortly petiolated); cubito-anal area max. 1.2 mm wide; CuA long, with numerous posterior branches (8 are preserved, but probably there were at least 10); CuA ends on the level of the nodus; MP ends far distal of the level of the nodus, with numerous short posterior secondary branches at its distal end; postdiscoidal area narrow with only a single row of cells in the basal part except for the two most basal cells which are double (width near discoidal triangle 1.4 mm; min. width in the constricted median part 1.1 mm; width at hind margin 4.1 mm); no Mspl, but numerous short posterior secondary branches at distal end of MA which reaches nearly the level of the pterostigma; RP3/4 and MA parallel with only one

row of cells between them, except distally were they diverge; numerous short posterior secondary branches at distal end of RP3/4 which reaches up to the level of the distal end of the pterostigma; first branching of RP (= midfork) 4.5 mm (right wing) or 4.2 mm (left wing) basal of subnodus (second branching of RP); IR2 originates on RP3/4 and reaches beyond the pterostigma; RP2 not aligned with subnodus, but originating on RP1/2 2.3 mm (right wing) or 2.0 mm (left wing) distal of subnodus and nearly reaching the wing apex; only one lestine oblique vein 'O' between RP2 and IR2, 2.8 mm (right wing) or 2.3 mm (left wing) and 2–3 cells distal of origin of RP2; about 7 bridge crossveins between RP2 and IR2 basal of RP2; RP3/4 and IR2 are divergent, with basally one row of cells in-between; no Rspl; RP1 and RP2 parallel with only one row of cells between them up to the level of the pterostigma; vein pseudo-IR1 is well-defined and originates on RP1 beneath the middle of the pterostigma; one row of cells between pseudo-IR1 and RP1.

Hindwing: Preserved length 27.6 mm (estimated total length about 29.0 mm); width at nodus 6.9 mm; distance from base to nodus 12.0 mm (the nodus is situated at about 41 % of the estimated wing length, thus in a rather basal position); distance from nodus to pterostigma 11.8 mm; the primary antenodal crossveins Ax1 and Ax2 are strong and bracket-like; Ax1 is 2.0 mm basal of Ax2, and Ax2 is 3.7 mm distal of the estimated wing base; apparently there were no secondary antenodal crossveins; several (at least 4) antesubnodal crossveins in the middle of the antesubnodal area; about 10 postnodal crossveins between nodus and pterostigma, non-aligned with the corresponding 9 postsubnodal crossveins; no "libelluloid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 2.6 mm long and max. 1.0 mm wide; its distal side is much more oblique than its basal side; the margins of pterostigma are very strongly thickened; the pterostigma is distinctly braced; the arculus is straight (the discoidal cell is basally closed by a short and curved crossvein); bases of veins RP and MA (sectors of arculus) widely separated at the arculus; the discoidal cell is transverse with an acute tip, and not divided into hypertriangle and triangle; MAb is 1.7 mm long and straight; a short but distinct pseudo-anal vein PsA (= AA0) delimits a (apparently unicellular) subdiscoidal triangle; basal space free; cubital and CuP-crossing not preserved; anal area not preserved; cubito-anal area max. 2.0 mm wide with 3 rows of cells; CuA long, with numerous (about 6) posterior branches; CuA ends on the level of the nodus; MP ends far distal of the level of the nodus, with numerous short posterior secondary branches at its distal end; postdiscoidal area narrow with only a single row of cells in the basal part (width near discoidal triangle 1.7 mm; min. width in the constricted median part 0.8 mm; width at hind margin 2.7 mm); no Mspl, but some short posterior secondary branches at distal end of MA which reaches nearly the level of the pterostigma; RP3/4 and MA parallel with only one row of cells between them, except distally were they diverge; numerous short posterior secondary branches at distal end of RP3/4 which reaches up to the level of the distal end of the pterostigma; first branching of RP (= midfork) 4.1 mm (right wing) or 3.9 mm (left wing) basal of subnodus (second branching of RP); IR2 originates on RP3/4 and reaches beyond the pterostigma; RP2 not aligned with subnodus, but originating on RP1/2 1.9 mm (right wing) or 1.7 mm (left wing) distal of subnodus and nearly reaching the wing apex; only one lestine oblique vein 'O' between RP2 and IR2, 2.7 mm (right wing) or 3.4 mm (left wing) and 3–4 cells distal of origin of RP2; about 6 bridge crossveins between RP2 and IR2 basal of RP2; RP3/4 and IR2 are divergent, with basally one row

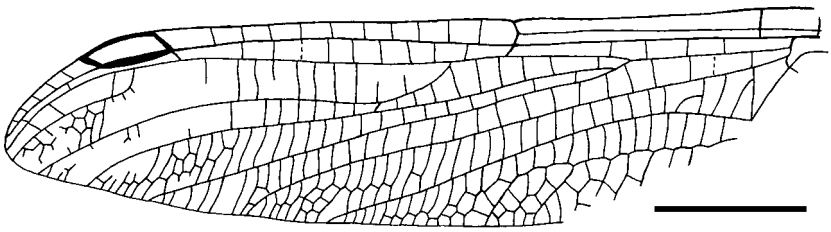

Fig. 3. *Parastenophlebia casta* n. comb., right hind wing from below; coll. BÜRGER, without number. – Scale bar: 5 mm.

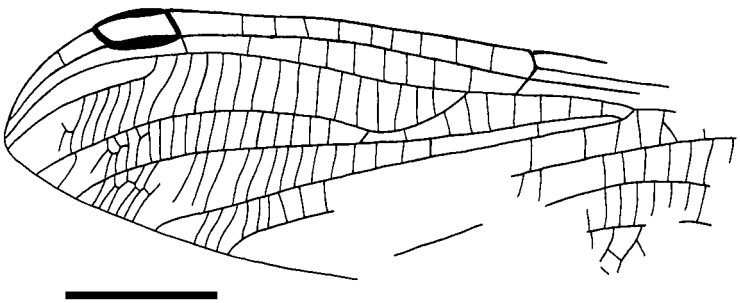

Fig. 4. *Parastenophlebia casta* n. comb., left hind wing from above (twisted); coll. BÜRGER, without number. – Scale bar: 5 mm.

of cells in-between; no Rspl; RP1 and RP2 parallel with only one row of cells between them up to the level of the pterostigma; vein pseudo-IR1 is well-defined and originates on RP1 beneath the middle of the pterostigma; one row of cells between pseudo-IR1 and RP1.

Specimen SOS 4656 JME (Fig. 6)

A completely preserved dragonfly of unknown sex from the locality Obereichstätt. No details of the wing venation are visible. Total body length 48.0 mm; width of head 6.0 mm; length of abdomen 33.0 mm; width of abdomen min. 1.3 mm and max. 4.9 mm at the distinct apical expansion; the legs are faintly visible as well, and apparently were rather short; wing length about 27.5 mm. This specimen was designated by FLECK et al. (2003) as neotype, because the much better preserved present specimen was in private collection.

Specimen BMMS 266a and b

Plate and counterplate of a completely preserved dragonfly of unknown sex from the locality Schernfeld. No details of the wing venation are visible. Total body length 44.2 mm; width of head 5.0 mm (eyes clearly separated); length of abdomen 33.0 mm; width of abdomen min. 1.1 mm and max. 5.2 mm at the distinct apical expansion; a few legs are faintly visible as well; wing length about 27 mm.

Specimen MA 237a and b in coll. STÖBENER (Figs 7–8)

A completely preserved dragonfly of unknown sex from the Solnhofen limestone. No details of the wing venation are visible. Total body length 47 mm; at the place of

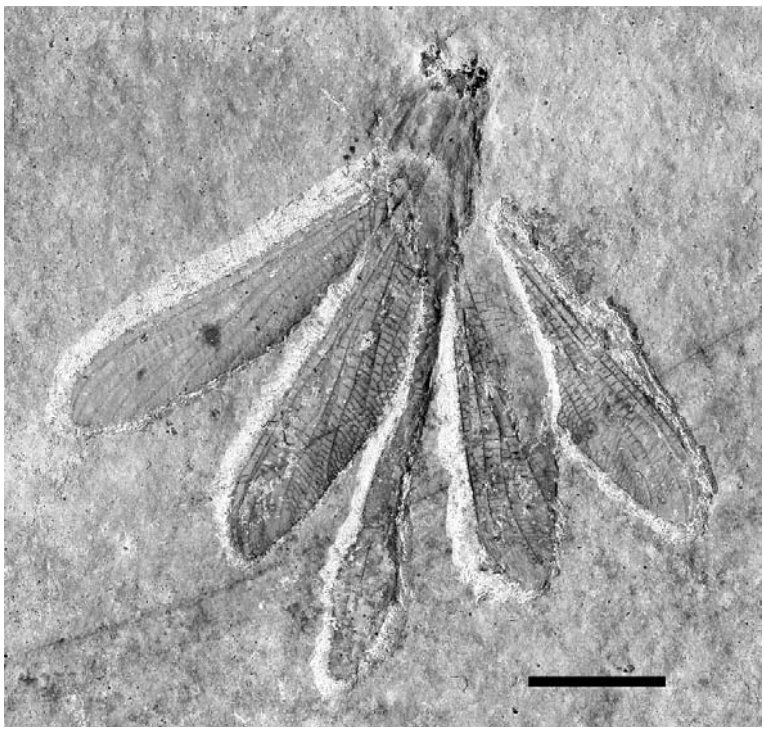

Fig. 5. *Parastenophlebia casta* n. comb.; coll. BÜRGER, without number. – Scale bar: 10 mm.

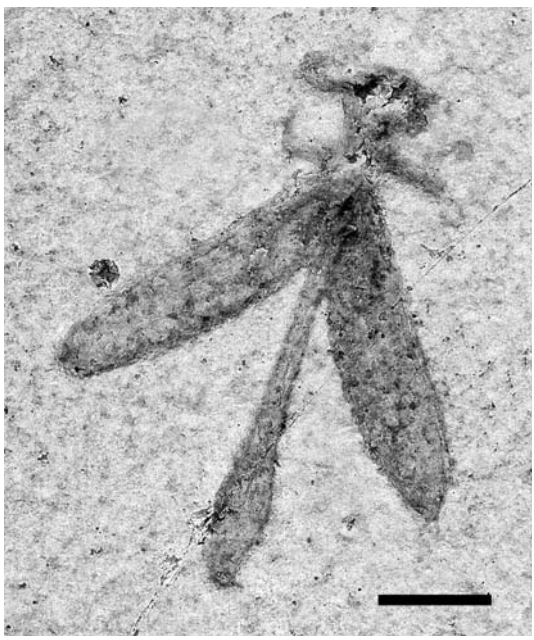

Fig. 6. *Parastenophlebia casta* n. comb.; neotype, Jura Museum Eichstätt, no. SOS 4656 (ex coll. SCHÄFER). – Scale bar: 10 mm (Photo: W. HARLING).

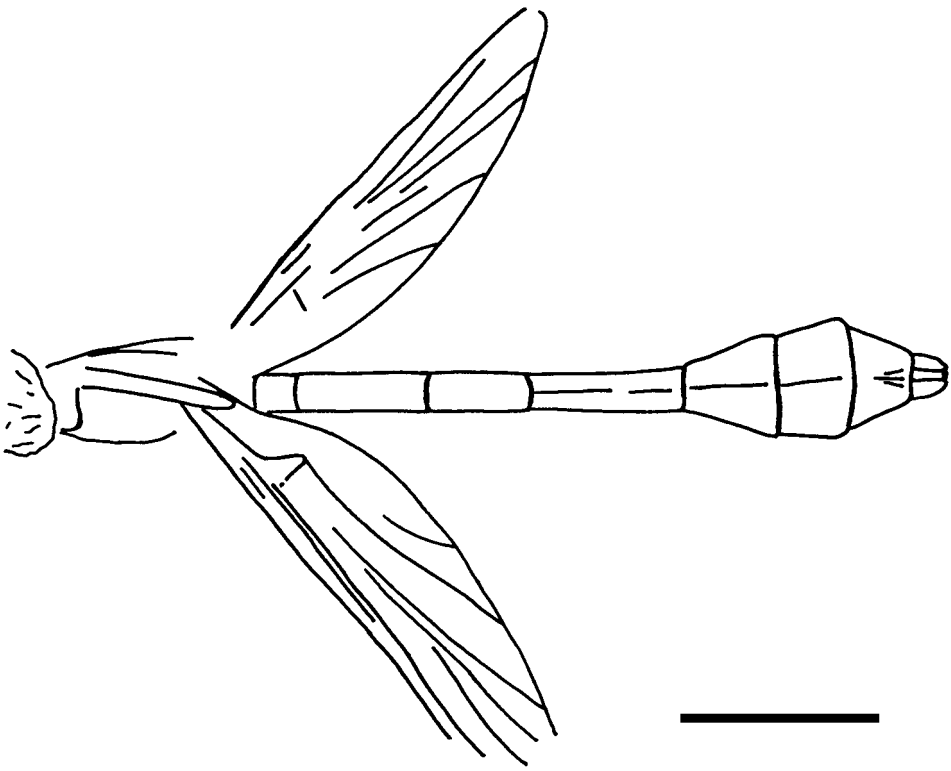

Fig. 7. *Parastenophlebia casta* n. comb.; coll. STÖBENER, no. MA 237a. – Scale bar: 10 mm.

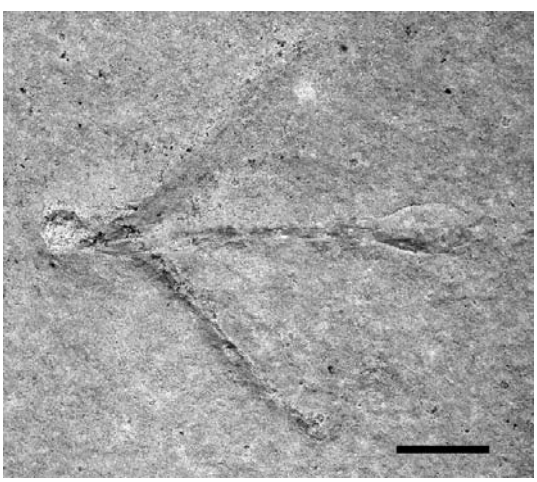

Fig. 8. *Parastenophlebia casta* n. comb.; coll. STÖBENER, no. MA 237a. – Scale bar: 10 mm (Photo: G. BECHLY).

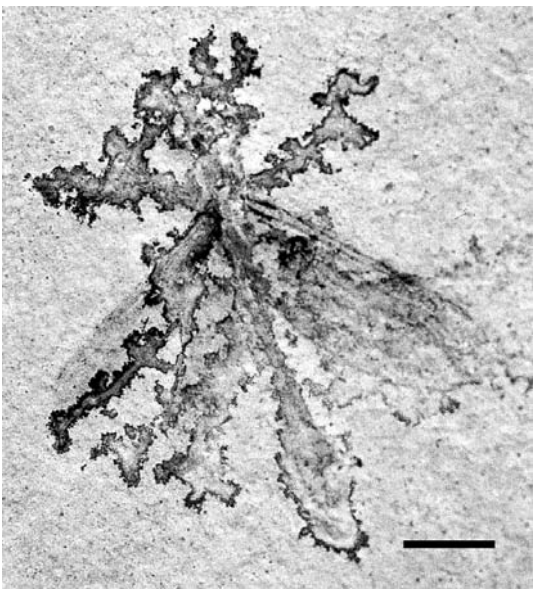

Fig. 9. *Parastenophlebia casta* n. comb.; coll. KOSCHNY, no. 0013. – Scale bar: 10 mm (Photo: G. KOSCHNY).

the head there is only a globular pit in the stone; width of abdomen min. 1.1 mm and max. 5.5 mm at the distinct apical expansion; the anal appendices are very short (1.5 mm) and broad (1.2 mm); the folded legs are faintly visible; wing length about 27 mm.

Specimen 0013 in coll. KOSCHNY (Fig. 9)

A completely preserved dragonfly of unknown sex from the Solnhofen limestone. No details of the wing venation are visible. Total body length 48 mm; wing length of the forewings is 29–30 mm and of the hind wings 30 mm; width of the forewings 6 mm and of the hind wings 7 mm.

4. Phylogenetic position

Parastenophlebia casta does not share any important synapomorphies with Stenophlebiidae. The common expanded end of the abdomen is also occurring as convergence in Gomphides and Liassophlebiidae, and therefore no sufficient evidence for a close relationship. The wings being preserved obliquely directed backwards is a typical feature of most representatives of the "anisozygopteroid" grade and e. g. also common in Isophlebioidea and Tarsophlebiidae. The transverse triangles mentioned by HANDLIRSCH (1906) are obviously based on a misinterpretation of the discoidal cell of this species, which is not even divided into a triangle and hypertriangle in both pairs of wings. *Parastenophlebia casta* does indeed share the three synapomorphies of Stenophlebioptera (= Gondvanogomphidae + Stenophlebiidae) mentioned by BECHLY (1996, 2002):

1.) IR2 and RP3/4 arising close together, correlated with a very long and narrow bridge space.
2.) Base of RP2 not strictly aligned with subnodus (more probably a symplesiomorphy).
3.) Cubito-anal area of hind wings reduced, thus both wings of similar shape.

However, these characters are rather weak anyway, and thus do not outweigh the stronger evidence for a position within Heterophlebioidea. Furthermore, FLECK et al. (2003) demonstrated that the monophyly of Stenophlebioptera is doubtful at least: The alignment of RP2 with the subnodus is variable in Heterophlebioptera (e. g. in *Heterophlebia buckmanni* (BRODIE, 1845), *Paraheterophlebia marcusi* NEL & HENROTAY, 1993, and *Myopophlebia libera* BODE, 1953), and a far distal displacement of the origin of RP2 also occurs in *Grimmenopteron elegantulum* ANSORGE, 1996. The elongation of the bridge space is of course correlated with the displacement of RP2, and the bridge space is not narrow in *Parastenophlebia casta*, contrary to Stenophlebioptera. Likewise the reduction of the cubito-anal area of the hind wing is less pronounced in *Parastenophlebia casta* and could easily be the result of convergence, and there is no evidence that the hind wing was petiolated as in Stenophlebiidae.

The most important argument against a relationship with Stenophlebioptera is the absence of any synapomorphies of Parastenophlebiidae n. fam. with Trigonoptera and especially the plesiomorphic presence of an open forewing discoidal cell, which clearly excludes a close relationship with Stenophlebioptera as subordinated taxon within Trigonoptera.

On the other hand, an attribution to Epiproctophora can be considered as very well supported because of several strong synapomorphies (viz costal margin not indented at nodus; arculus shifted basally in a position between the two primary antenodals Ax1 and Ax2; discoidal cell distally distinctly widened in hind wing, correlated with a much less oblique distal side MAb than in the forewing). The presence of a pseudo-anal vein PsA allows an attribution to Euepiproctophora (= Epiophlebiidae + Anisopteromorpha). The vein M+Cu being distinctly bent near the arculus is a synapomorphy with Anisopteromorpha; the lack of a division of the hind wing discoidal cell in hypertriangle and triangle is no conflicting evidence, because it is also lacking in Liassophlebiidae. The unique shape of the forewing discoidal cell that is very transverse and narrow is a putative synapomorphy with Heterophlebioptera (however, the monophyly and internal phylogeny of this group is still doubtful according to FLECK et al. 2003), as well as the short petiolation of the forewing and the expanded apex of the abdomen which is also known from *Liassophlebia clavigaster* (Liassophlebiidae) and *Paraheterophlebia marcusi* (Myopophlebiidae).

The following putative synapomorphies suggest an attribution to Heterophlebioidea: Antenodal crossveins between costal margin and ScP suppressed distal of Ax2; IR2 arising on RP3/4; in the forewing the distal side MAb of the discoidal cell is shifted somewhat distally of the arculus. Within Heterophlebioidea, Parastenophlebiidae n. fam. might be closer related to Liassophlebiidae with which they share the open forewing discoidal cell and undivided hind wing discoidal cell as two symplesiomorphies. However, Parastenophlebiidae n. fam. lacks all autapomorphies of Liassophlebiidae, and also does not show any synapomorphies with other Heterophlebioptera, except for the poorly known liassophlebiid (?) genus *Grim-*

menopteron which shares the suppression of all secondary antenodals and the very distal displacement of the origin of RP2. Considering the uncertain affinities within Heterophlebioidea and the unique pattern of the wing venation, the erection of a separate new family seems to be justified.

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