Revision and phylogenetic affinities of the Jurassic Steleopteridae Handlirsch, 1906 (Odonata: Zygoptera)

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The Jurassic odonate family Steleopteridae is revised. Two new genera and species *Parasteleopteron guischardi* and *Euparasteleopteron viohli* are described. The phylogenetic affinities of this group are discussed. The Steleopteridae are excluded from the Epiproctophora and transferred into the Zygoptera (stemgroup). *Euphaeopsis multinervis* is redescribed and transferred to Epiproctophora: Isophlebioidea, and the genus *Pseudoeuphaea* with its four species is considered as a nomen dubium in Odonata incertae sedis.

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Introduction

The Steleopteridae Handlirsch, 1906 is a small family of very slender damselfly-like Odonata, known by four genera from the Upper Jurassic of Germany and Kazakhstan. This enigmatic group has been generally considered as Zygoptera (Handlirsch 1906; Fraser 1938; Pritykina 1968; Nel & Paicheler 1993), maybe close to the Amphipterygidae. Bechly (1996) tentatively transferred this taxon into the Epiproctophora (= 'Anisozygoptera' + Anisoptera), but also noted 'that it cannot be excluded that Steleopteridae could be related to basal Caloptera like Sieblosiidae'. We recently had the opportunity to examine all known material of Steleopteridae, i.e. the holotype of *Steleopteron deichmuelleri* Handlirsch, 1906, two specimens of *Auliella crucigera* Pritykina, 1968 (including the holotype) and the holotypes of *Parasteleopteron guischardi* gen. and sp. n. and *Euparasteleopteron viohli* gen. and sp. n., as well as several further specimens of Steleopteridae from Solnhofen limestone. After the study of this material, it became clear that nearly all putative synapomorphies of Steleopteridae with Epiproctophora are erroneous or dubious. Therefore, a new discussion on the phylogenetic position of this group was necessary and is provided in this work. Furthermore, we discuss the genera *Euphaeopsis* Handlirsch, 1906 and *Pseudoeuphaea* Handlirsch, 1906 that have recently been associated with Steleopteridae (e.g. Bechly 1999; Nel unpubl.).

Family **STELEOPTERIDAE** Handlirsch, 1906

Type genus. – *Steleopteron* Handlirsch, 1906.

Other included genera. – *Parasteleopteron* gen. n., *Euparasteleopteron* gen. n., and *Auliella* Pritykina, 1968. The genera *Euphaeopsis* Handlirsch, 1906 and *Pseudoeuphaea* Handlirsch, 1906 are based on very poorly described and figured specimens. We do not longer consider them as members of this family (see below).

New diagnosis. – (1) Presence of a unique structure of the cells in certain areas of the wings (autapomorphy): More precisely, in *Steleopteron*, some of the cells of the distal half of the wing are highly specialised. These cells occur in the areas between MP and the posterior wing margin, between MA and RP3/4, and between RP3/4 and

IR2. The transverse veins that delimit the cells between the main veins are distinctly convex, but one or more small concave veins cross these cells. The development of this structure is 'progressive' (see Fig. 1b), i.e. '1' the more proximal cells have no special structure; '2' some cells have a slight concavity, but no definite concave vein crosses them; '3' a small concave transverse vein is present in the middle of the cell; '4' the concavity of this small vein becomes more visible and a perpendicular less concave vein crosses through it; '5' the concavity of these two crossing veins is accentuated; '6' lastly, the cell is divided into four small cells, but its real limits are still visible because the outer veins are convex and the inner veins are still concave. This structure is very different from the usual division of a cell into smaller cells that occurs in all other odonatoid wings, i.e. the formation of a new row of cells in a area between two longitudinal main veins is accomplished by the division of a crossvein into two small branches that have the same convexity (or concavity). In *Parasteleopteron* gen. n. and *Euparasteleopteron* gen. n. only the cells of type '6' are present in the same areas. In *Auliella*, cells of type '5' and '6' are present in the area between MP and posterior wing margin. (2) Wing bases with a very long petiole. (3) An elongate discoidal cell, with the distal side strongly oblique, of different shape in the fore- and hindwing. (4) Pterostigmal brace not very distinct (except in *Euparasteleopteron*). (5) Numerous secondary antenodal crossveins. (6) Arculus in a distal position relatively to the primary antenodals (*Auliella*), or aligned with Ax2 (*Euparasteleopteron*). (7) Veins CuA and MA distally zigzagged and vanishing (autapomorphy). (8) Lestine oblique vein 'O' present (plesiomorphy). (9) Wings long and slender. (10) Bases of RP3/4 and IR2 midway between nodus and arculus. (11) Thorax small compared to the sizes of the wings and the abdomen. (12) Abdomen very long (but not gracile), distinctly extending beyond the wings (autapomorphy). (13) Ovipositor apparently complete, but without styli, very long, extending well beyond the abdomen (autapomorphy). (14) Ventrolateral longitudinal carina on the abdominal tergites present. (15) Longitudinal carina on the abdominal sternites absent. (16) The tenth abdominal segment is as long as the ninth (distinctly shorter in modern Zygoptera and Anisoptera) (autapomorphy?). (17) The first abdominal segment long, distinctly longer than in other Odonatoptera (autapomorphy?).

Genus ***Steleopteron*** Handlirsch, 1906

Type species. – *Steleopteron deichmuelleri* Handlirsch, 1906, by monotypy.

New diagnosis. – The specialised wing cells described in the familial diagnosis are of type '1' to '6', in the areas between MP and posterior wing margin, MP and RP3/4 and IR2 and RP3/4; vein IR2 with a very strong curvature at the level of the pterostigma; three rows of cells in the area between MP and posterior wing margin.

Steleopteron deichmuelleri Handlirsch, 1906

(Fig. 1-5)

Steleopteron Deichmülleri (sic) Handlirsch, 1906: 598, pl. XLVII, fig. 20-22.

Steleopteron deichmuelleri: Calvert 1913: 246, 249, 251, 253-255 (morphology); Fraser 1938: 141-143, fig. 3 (transferred to Amphipterygidae); Fraser 1957: 70 (in Amphipterygidae Amphipteryginae); Pritykina 1968: 35-36 (in Steleopteridae); Ponomarenko 1985: 136 (list, in Amphipterygidae); Carpenter 1992: 87 (in Steleopteridae); Nel & Paicheler 1993: 382-383 (discussion on affinities); Bechly 1996 (phylogenetic position of the family).

Steleopteron deichmulleri (sic): Bridges 1994: VII.65 (list).

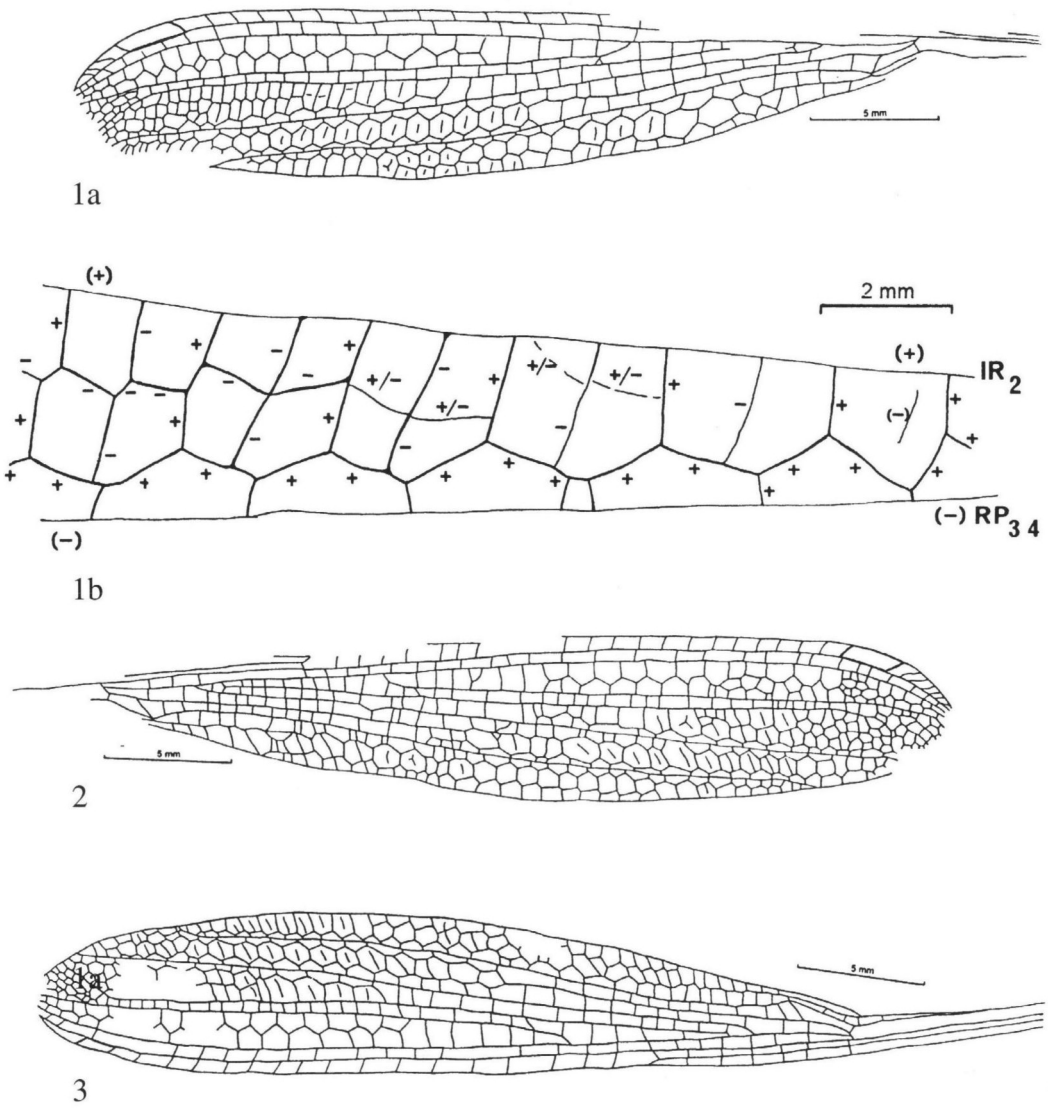
Material. – Holotype female specimen n° 1903.V.3 1985/4, Museum of Natural History in Vienna (Ponomarenko & Schultz 1988). Frickhinger (1994: fig. 258) figured an undescribed specimen from a German private collection (coll. Bürger, Bad Hersfeld) that he attributed to *Steleopteron deichmuelleri*, but it is too large for an attribution to this species, the nearly equal length of wings and abdomen would contradict a placement in Steleopteridae, and its wing venation suggests that it could rather be a Protomyrmeleontidae.

Stratum typicum. – Upper Jurassic, Malm zeta 2b ('oberer Weißjura'), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

Locus typicus. – Solnhofen, southern Frankonian Alb, Bavaria, Germany.

Redescription of holotype. – The descriptions and figures of Handlirsch (1906) and Fraser (1938) are incomplete and not precise, so that a redescription is necessary.

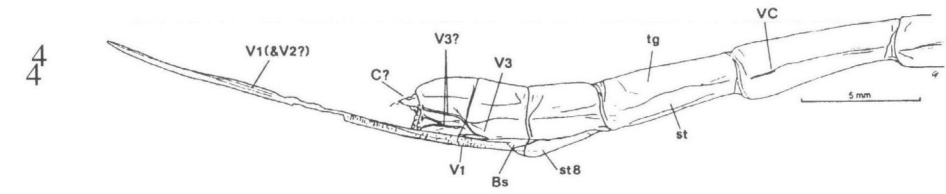
A thorax with three legs and two very similar wings in connection, a third wing and a leg near the thorax. The abdomen is visible 4 cm on the left. The wings are of two types, but it is difficult to determine which is the forewing or the hindwing.

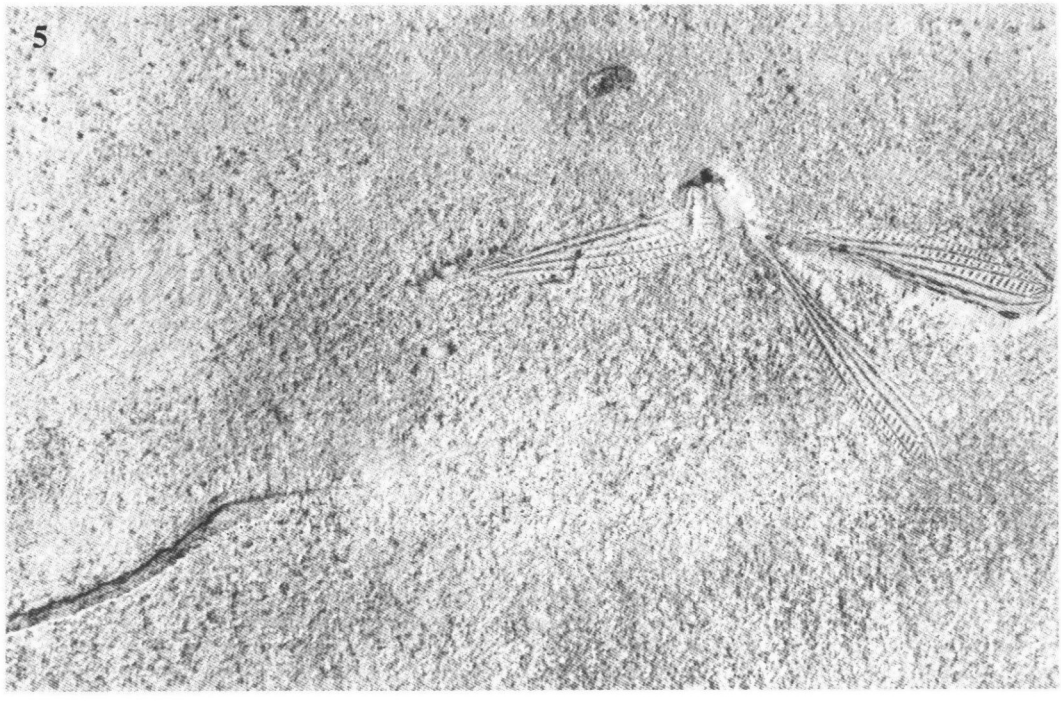


Figures 1-3. *Steleopteron deichmuelleri* Handlirsch, 1906, holotype specimen 1903.V.3 1985/4: (1a) Forewing (wing A) separated from the body. (1b) Same, detail of the organization of the cells in the area between RP3/4 and IR2. (2) Forewing (wing B) attached to the body. (3) Hindwing (wing C) attached to the body.

Head. A structure is present, 15.0 mm of the thorax, looking like an Odonata head. It is transverse, about 7 mm long and 3.5 mm wide. Two semi-globular structures are present, 2.5 mm wide, which could correspond to the eyes. This structure could be the transverse head of this specimen, with the eyes well separated.

Thorax. The thoracic skewness is well pronounced. Angle x, 60° (sensu Needham & Anthony 1903). Length of the thorax, about 7 mm. Legs. They are short. Femora 4.0 mm long and 0.8 mm wide. Tibia 4.0 mm long and 0.8 mm wide. Tarsi relatively long, 3.0 mm long. Spines not visible.





Figures 4-5. *Steleopteron deichmuelleri* Handlirsch, 1906, holotype specimen 1903.V.3 1985/4: (4) Five last abdominal segments and ovipositor; Bs, basivalvula; C, cercus; tg, tergite; st, sternite; st8, developed sternite 8; VC, ventral carina; V1, V2 and V3, valvulae 1, 2 and 3. (5) Photograph of holotype specimen (without scale).

Wings (Fig. 1-3). The two wings 'A' and 'B' are identical, but the wing 'C' is longer, with a different shape of the discoidal cell (distinctly longer), and a shorter pterostigma. Because it is longer, wing 'C' could be a forewing, as it frequently occurs in Odonata. Wings 'A' and 'B' are 39 mm long and 6 mm wide; width at the level of the nodus, 4.4 mm. Length of the petiole, about 7.5 mm, width, 1.3 mm. Wing 'C' is 40 mm long and 6 mm wide; width at the level of the nodus, 4 mm. Length of the petiole, 8 mm, width, 1.3 mm. Position of CuP not very clear, but apparently just distal separation between AA and AP. AA very straight before reaching CuA, at level of posterior angle of subdiscoidal cell. Arculus at 8.1 mm from wing base (wing 'C'), of similar structure on three wings: RP separating from MA a little basal of point of contact between RP+MA with posterior part of arculus. Discoidal cells free of crossveins, closed and quadrangular trapezoidal, with distal sides very oblique, not parallel with proximal sides. Discoidal cells of wings 'A' and 'B', although similar to that of wing 'C', more narrow and shorter. Length of costal side of discoidal cell of wing 'A', 1.4 mm, of distal side, 0.8 mm, of proximal side, 0.4 mm, of posterior side, 2.0 mm. Length of costal side of discoidal cell of wing C, 1.9 mm, of distal side, 0.9 mm, of proximal side, 0.3 mm, of posterior side, 2.7 mm. Subdiscoidal spaces very long and narrow, crossed by two

crossveins on wing 'C' and maybe free on wings 'A' and 'B'. Only one row of cells in cubito-anal area, below subdiscoidal cell. CuA separating from MP at posterior angle of discoidal cell, very short before its fusion with AA. Cubito-anal area gradually widened. CuA strongly zigzagged and vanishing distally. One row of cells in area between CuA and MP. Three rows of cells in cubito-anal area and in area between MP and posterior wing margin. This area is very long because MP reaches wing margin in distal half of wing, opposite pterostigma, at about 86 % of whole length of wing (wing 'C'). No definite branch of MP in area between MP and posterior wing margin. Area between MP and MA proximally broadened near discoidal cell, narrower distally, with one row of cells between MP and MA. MA proximally strong and straight, but distally zigzagged and vanishing in area between MP and RP3/4. MA never reaching posterior wing margin as an independent distinct vein. Only one row of cells in area between MA and RP3/4, distally narrowing. RP3/4 and IR2 branching on RP, about midway between arculus and nodus, on all wings. Distance between RP3/4 and arculus, 3.0 mm on wing 'A', on wing 'C', 3.7 mm. Distance between arculus and nodus on wing 'A', 8.1 mm, on wing 'C', 8.0 mm. Antenodal areas crossed by about six visible antenodal crossveins, more or less aligned with crossveins between ScP and RA. Two primary antenodal crossveins not preserved on all wings. Antenodal area between ScP and Costa never widened. Only four Bq crossveins in area between IR2, RP and base of RP2 (wing 'C'). Area between arculus and nodus, between RP and RA crossed by six crossveins (wing 'C'). One row of cells in area between RP3/4 and IR2 in its proximal part, but distally broadened and narrowed near posterior wing margin, opposite pterostigma, with four rows of cells in its broadest part. IR2 straight except near its apex, where it is abruptly curved and vanishing in area between RP3/4 and RP2, opposite pterostigma. Nodus poorly preserved, but costal margin basal of nodus apparently aligned with costal margin distal of nodus. Nodal vein Cr is weakly oblique and well aligned with subnodus. Postnodal area very long, with about sixteen postnodal crossveins on wing 'C' and about twenty-two on wings 'A' and 'B', some of them being weakly curved and not aligned with corresponding crossveins between RA and RP1. Base of RP2 well distal of subnodus, 3.0 mm on all wings. One row of cells in area between RP2 and IR2 in its main part, but it is distally widened, with few small branches of RP2 near wing apex. RP2 reaching exactly wing apex. RP2 very straight. A small distinct oblique vein 'O' between RP2 and IR2, one or two cells distal of subnodus. Base of IR1 about five to six cells distal of that of RP2. IR1 zigzagged and more or less distally vanishing in area between RP2 and RP1, at level of pterostigma. Area between RP2 and RP1 narrow, two or three cells wide in its broadest part, without any secondary longitudinal veins. It is distally narrowing near wing apex (only two cells wide at wing apex). Pterostigma well defined and sclerotized, shorter on wing 'C' than on wings 'A' and 'B', 1.2 mm long and 0.4 mm wide on wing 'C', and 2.1 mm long and 0.6 mm wide on wings 'A' and 'B'. Pterostigma not braced, covering two cells and a half on wings 'A' and 'B' and one cell on wing 'C'. Distance between pterostigma and nodus, 21.3 mm on all wings, between pterostigma and apex, 2.1 mm on wing 'C', 3.2 mm on wings 'A' and 'B'. No secondary zigzagged longitudinal small vein in post pterostigmal area.

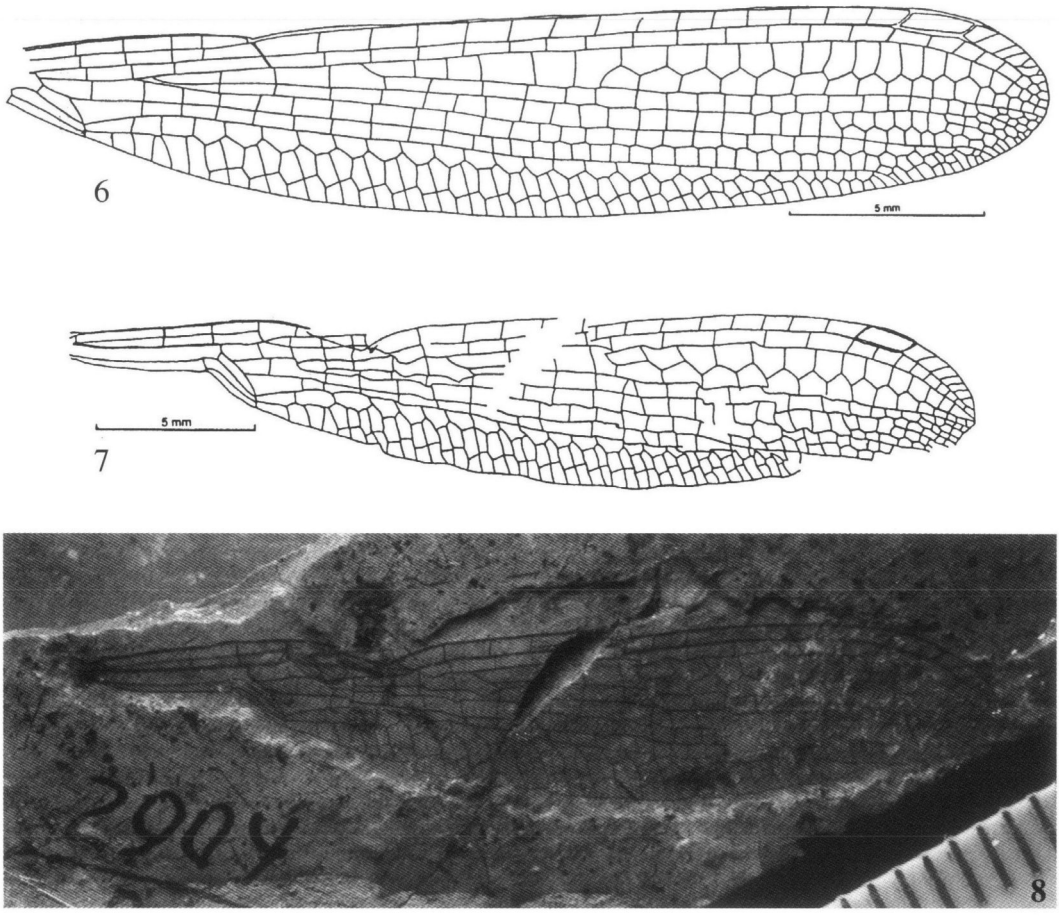
Abdomen (Fig. 4). Complete, about 50 mm long, width, 2.0 mm. As the abdomen is fossilised on its side, only half of each tergite are visible. The anterior carina of the tergites seems to be absent. Ventro-lateral carina of the tergites (sensu Asahina 1954) present. Posterior carina entire and deeply indicated. No transverse carina on every segment. Surfaces of tergites covered with small transverse grooves, as in modern *Lestes* spp. or *Calopteryx* spp. Tenth abdominal segment as long as ninth.

Genital organs (Fig. 4). A very long slightly curved ovipositor, about 20 mm long, very sharp at the apex, and transversely striated. This ovipositor begins on the disto-ventral part of the eighth segment and is made of the two visible joined long valvula 1 (sensu Pfau 1991). Valvula 2 of ninth segment probably present, although not directly visible, hidden under the hypertrophied valvula 1. Valvula 3 disposed on an apical extension of tenth segment, but with absolutely no styli.

Genus ***Auliella*** Pritykina, 1968

Type species. – *Auliella crucigera* Pritykina, 1968, by subsequent designation.

Diagnosis. – The specialised wing cells described in the familial diagnosis are of types '5' and '6', and only present in the area between MP and pos-



Figures 6-8. Wing, *Auliella crucigera* Pritykina, 1968: (6) Holotype specimen PIN 2066/301. (7) Specimen PIN 2904/8. (8) Photograph of same (scale as indicated by ruler).

terior wing margin and along the wing margin in the area between MP and RP3/4; only three rows of cells between MP and posterior wing margin; IR2 with no strong distal curvature.

Auliella crucigera Pritykina, 1968

(Fig. 6-8)

Auliella crucigera Pritykina, 1968 : 35-36, text-fig. 8, pl. 2, fig. 4 ; Carpenter 1992: 87; Bridges 1994: VII.61 (list).

Ambiella cruciqera (sic): Nel & Paicheler 1993: 383 (subsequent incorrect spelling).

Material. – Holotype specimen n° PIN 2066/301, an isolated wing with a broken petiole. Further specimen n° PIN 2904/8, an isolated but complete wing.

Stratum typicum. – Upper Jurassic, Callovian-Kimmeridgian or Oxfordian-Kimmeridgian (Zherikhin & Gratshev 1993; Mostovski & Martínez-Delclòs 2000).

Locus typicus. – Karatau, Chimkent region, Southern Kazakhstan, C.E.S.

Redescription. – This redescription is based on the holotype and the second mentioned specimen.

Wing, 29.3 mm long and 5.4 mm wide (PIN 2904/8). Wing petiolate, petiole length, 4.4 mm. AA separating from AP just basal of CuP. RP separating from MA a little basal of point of contact

between RP + MA and posterior part of arculus. Discoidal cell close, quadrangular, with distal side very oblique, not parallel with proximal side. Length of costal side of discoidal cell, 0.7 mm, of distal side, 0.7 mm, of proximal side, 0.3 mm, of posterior side, 1.4 mm (holotype). Length of costal side of discoidal cell, 1.0 mm, of distal side, 0.8 mm, of proximal side, 0.25 mm, of posterior side, 1.7 mm (PIN 2904/8). Discoidal cell of PIN 2904/8 distinctly narrower than that of

Holotype. Discoidal cell free of crossveins. Subdiscoidal space very long and narrow, 2.2 mm long and 2.0 mm wide (PIN 2904/8), free of crossveins. Anal area, below subdiscoidal cell, one cell wide. CuA separating from MP at posterior angle of discoidal cell. Cubito-anal area gradually widened, but CuA distally vanishing. One row of cell in area between CuA and MP. Always three rows of cells in area between MP and posterior wing margin. MP reaching posterior wing margin in distal half of wing, 24 mm distal of its base and at about 81 % of the whole wing length. Cells in area between MP and posterior wing margin crossed by a concave small vein in their median part. One row of cells in area between MP and MA, basally broadened, but distally narrower and widened again only very close to wing margin. MA proximally strong and straight zigzagged in its distal half, but never vanishing in area between MP and RP3/4. MA reaching posterior wing margin as a distinct vein. One row of cells in area between MA and RP3/4, distally narrowing. Base of RP3/4 and IR2 about midway between arculus and nodus, distance between RP3/4 and arculus, 2.4 mm. Distance between arculus and nodus, 5.5 mm. Antenodal area crossed by four visible antenodal crossveins distal of level of arculus, nearly aligned with crossveins between ScP and RA. Two primary antenodal veins Ax1 and Ax2 well preserved, Ax2 being distinctly basal of arculus. Antenodal area, between ScP and Costa, not widened. Three or four Bq crossveins in space between IR2, RP and base of RP2. Area between arculus and nodus, between RP and RA with three crossveins. One row of cells in area between RP3/4 and IR2 in its proximal part, but broadened distally just basal of level of pterostigma, four cells wide in its broadest part. Subnodus oblique, an oblique nodal vein Cr well aligned with subnodus. Postnodal area long, with fourteen postnodal crossveins, the most distal ones not being aligned with corresponding crossveins between RA and RP1. Base of RP2 two cells distal of subnodus. One row of cells in area between RP2 and IR2, broadened distal of level of pterostigma, with few small branches of RP2 and IR2 curved towards posterior wing margin near wing apex. RP2 straight, reaching wing apex. A small distinct oblique vein 'O' between RP2 and IR2, one cell distal of subnodus. Base of IR1 about six cells distal of that of RP2, IR1 zigzagged. Two rows of cells in area between RP1 and RP2 in broadest part. Pterostigma well defined, 2.0 mm long and 0.7 mm wide in both wings, covering two cells and not clearly basally braced. Distance between pterostigma and nodus, 16.2 mm. Distance between pterostigma and apex, 2.7 mm (holotype) and 3.2 mm (PIN 2904/8). Post-pterostigmal area, between Costa and RA without any secondary zigzagged longitudinal vein, but with some Y-shaped crossveins.

Genus ***Parasteleopteron*** **gen. n.**

Type species. – *Parasteleopteron guischardi* sp. n.

Etymology. – After the Greek word 'para' and the genus *Steleopteron*.

Diagnosis. – The specialised wing cells described in the familial diagnosis are of type '6', in the areas between MP and posterior wing margin, between MP and RP3/4, and between RP3/4 and IR2; six rows of cells between MP and posterior wing margin; IR2 with no strong distal curvature. The differences with *Euparasteleopteron* gen. n. are listed in the diagnosis of this latter genus.

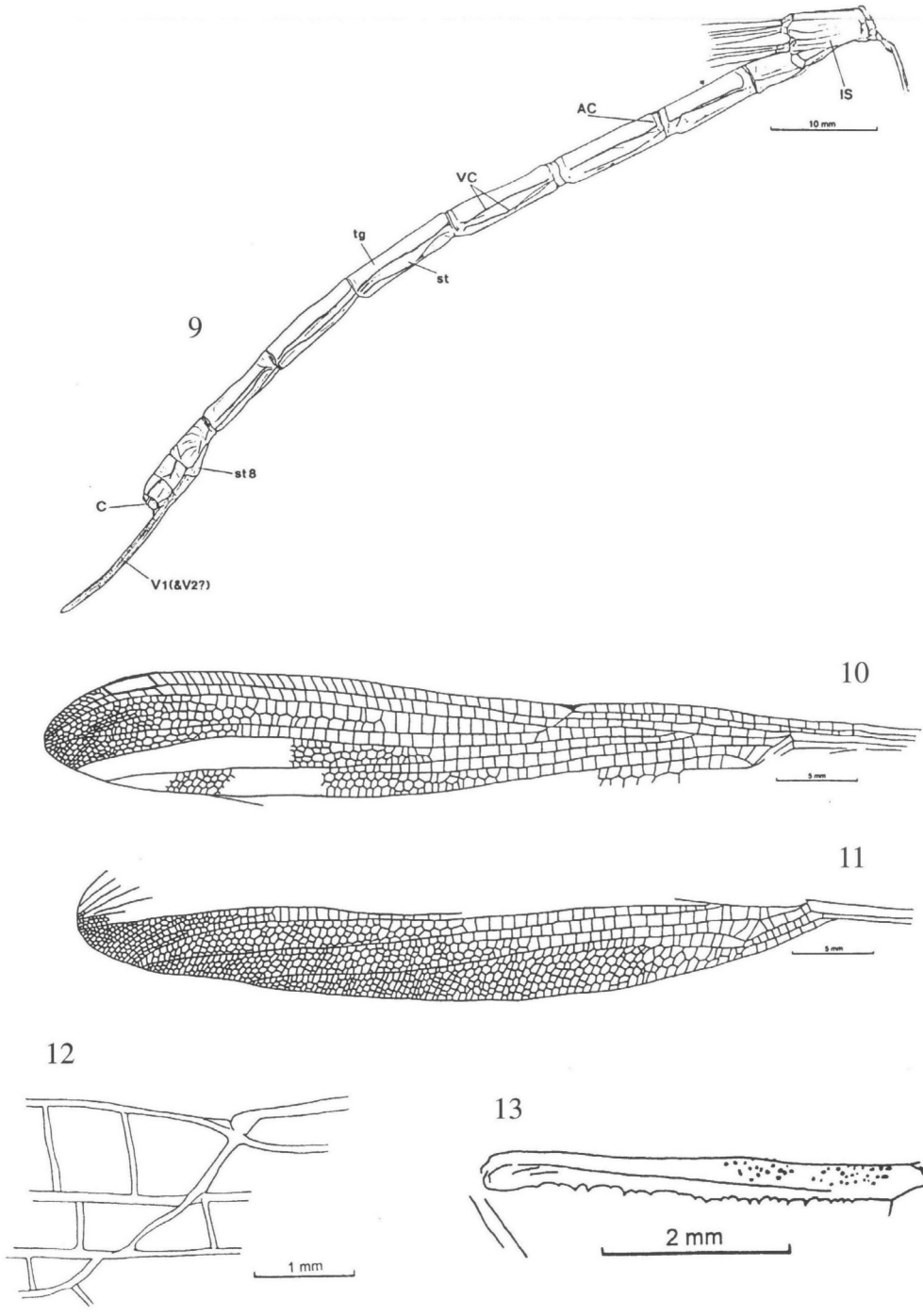
Parasteleopteron guischardi **sp. n.**

(Fig. 9-14)

'*Euphaeopsis multinervis* (Hagen) 1862': Frickhinger 1994: 134, fig. 250 (figured).

Material. – Holotype female specimen n° SOS 3615 (1937 No. 3 BK a,b), labelled as 'Euphaeopsis multinervis', Jura Museum, Eichstätt, Germany (Fig. 9-14). Paratype female? specimen n° SMNS 64436 (old number GB47), Staatliches Museum für Naturkunde Stuttgart, Germany (ex coll. Ludwig).

Frickhinger (1994: fig. 257) figured this specimen erroneously as *Pseudoeuphaea filosa* and incorrectly stated it to be in coll. Leich. Size and visible wing venation clearly suggest that it belongs to *Parasteleopteron guischardi*. A further female specimen (part and counterpart) without number is in the German private coll. Seppelt (Hildesheim) (ex coll. Krauss, Weissenburg, who may still have the counterpart). The latter specimen has a wing length of about 60 mm and a total body



Figures 9-13. *Parasteleopteron guischardi* gen. and sp. n., holotype specimen SOS 3615: (9) Body structures; AC, anterior carina; C, cercus; IS, thoracic interpleural suture; tg, tergite; st, sternite; st8, developed sternite 8; VC, ventral carina; V1 and V2, valvulae 1 and 2. (10) Forewing. (11) Hindwing. (12) Forewing nodus. (13) Femur 2 or 3.

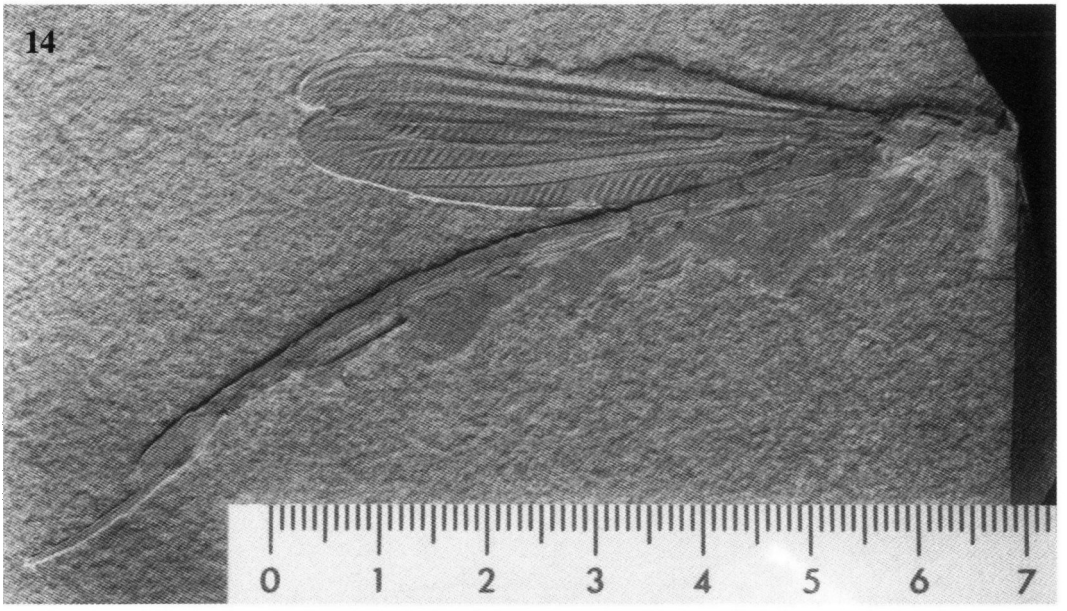


Figure 14. Photograph, *Parasteleopteron guischardi* gen. and sp. n., holotype specimen SOS 3615 (part) (scale as indicated by the ruler).

length (incl. ovipositor) of about 105 mm. It shows a curious structure beneath the distal abdomen that is not visible in any other specimen of Steleopteridae: this structure might either represent a very elongated valvula 3 of the ovipositor, but more probably an artefact since its apparent origin may be to proximal for a part of the ovipositor.

Etymology. – After Mr Daniel Guischard (Frankfurt a. M.), cousin of the third author (G.B.).

Stratum typicum. – Upper Jurassic, Malm zeta 2b ('oberer Weißjura'), Lower Tithonian, Hybonotum-Zone, Solnhofen Lithographic Limestone.

Locus typicus. – Langenaltheimer Haardt quarry, Eichstätt, southern Frankonian Alb, Bavaria, Germany.

Diagnosis. – That of the genus.

Description. – It is mainly based on the holotype specimen (Fig. 9-16). Part and counterpart of a nearly complete specimen fossilised on its side, with the four wings partly overlapping. The head is missing on the part and partly but poorly preserved on the counterpart. The thorax is poorly preserved. The costal part of the hind wings and the posterior part of the fore wings are partly destroyed. The venation is in a good state of preservation. The abdomen is very well preserved. There is no trace of coloration.

Thorax (Fig. 9). Thoracic skewness well pronounced. Angle x, more than 50° (sensu Needham & Anthony 1903). Length of thorax, 10.0 mm, width at level of wing base, 6.0 mm. Interpleural suture between meso- and metathorax probably complete (dorsal part present).

Legs (Fig. 13). Only one is partly preserved (femora + part of tibia). It is impossible to determine whether it is a meso- or metathoracic leg. Femora 10.0 mm long and 0.8 mm wide, with a longitudinal ridge, small punctures in its proximal part and small denticulations or bases of spines (?) along its inner margin. The tibia does not show any useful details.

Abdomen (Fig. 9). It is very long, 75.0 mm long and 4.0 mm wide, 23.0 mm longer than wings. Length of first segment, 4.0 mm, of second segment, 10.0 mm, of third, fourth, fifth and sixth segments, 11.0 mm, of seventh segment, 9.0 mm, of eighth segment, 4.0 mm, of ninth segment, 2.0 mm, of tenth segment, 2.0 mm. First segment comparatively longer than those of other fossil and modern Odonata. Since the abdomen is fossilised in a latero-ventral position, only half of

each tergite is visible. Ventro-lateral longitudinal carina (sensu Asahina 1954) of tergites present. Longitudinal carina of sternites absent. A deeply indicated posterior carina on tergites. No transverse carina on all segments. Surfaces of tergites covered with small transverse grooves, as in modern *Lestes* spp. or *Calopteryx* spp. Tenth abdominal segment as long as ninth.

Genital organs (Fig. 9, 14). A very long and slightly curved ovipositor, 22.0 mm long and 1.0 mm wide, extending 13.0 mm beyond abdomen. Eighth sternite well developed. Ovipositor beginning on disto-ventral part of eight segment and made of two joined long valvulae 1 (V1 sensu Pfau 1991). Second valvulae V2 of ninth segment not directly visible, hidden under hypertrophied valvulae 1 but there are longitudinal furrows in the distal part of the ovipositor, suggesting the presence of the valvulae 2 below V1. Valvulae 3 poorly visible. No visible styli. Such an ovipositor is very similar to that of *Steleopteron*. The presence of strong carinae on the broadened eighth, ninth, and tenth segments suggests the presence of strong muscles related to the ovipositor. One cercus is visible behind the median part of the tenth segment.

Wings (Fig. 10-12). The four wings are very similar in dimensions, proportions and shapes. Length, 55.0 mm; width, 7 to 8 mm. Wings all petiolate, with a long and narrow petiole, 7.0 mm long and 1.8 mm wide. AA separating from AP just before CuP in hindwing, but not well preserved in forewing. AA straight before reaching CuA, at posterior angle of subdiscoidal cell. Arculus 8.7 mm from wing base, similar in four wings: RP separating from MA exactly at point of contact between RP + MA with posterior part of arculus. Discoidal cells quadrangular, with distal sides very oblique, not parallel with proximal sides. Discoidal cell of forewing narrower, although similar to that of hindwing. Length of costal side of forewing discoidal cell, 1.5 mm, of distal side, 1.8 mm, of proximal side, 0.5 mm. Length of costal side of hindwing discoidal cell, 3.3 mm, of distal side, 1.6 mm, of posterior side, 4.8 mm, of proximal side, 0.6 mm. Hindwing discoidal cell crossed by four transverse veins, but since the forewing one is not very well-preserved, it is impossible to determine whether it was crossed or not. Hindwing subdiscoidal space very long and narrow, 5.5 mm long and 0.6 mm wide, crossed by nine crossveins. Forewing subdiscoidal space not well preserved. Anal area, below subdiscoidal space, one-cell wide. CuA separating from MP at posterior angle of discoidal cell, very short, 0.4 mm long before it is fused with AA. Cubito-anal area gradually widened. CuA vanishing distally, 7 to 8 mm distal of its base. Only one row of cells in area between CuA and MP. Cubito-anal area and distally area between MP and posterior wing margin three, five to six and distally six cells wide. This area is very long because MP reaches the posterior wing margin in distal half of wing, 31.5 mm from its base and at about 81 % of wing length. Area between MP and posterior wing margin filled with more than 60 alternatively concave and convex parallel small branches of MP, almost perpendicular to the posterior wing margin. Area between MP and MA basally broadened, but distally narrower and then widened again, with one row of cells for about 15 to 16 mm. MA proximally a strong and straight vein, but distally vanishing in area between MP and RP3/4. MA never reaching posterior wing margin as an independent distinct vein. One row of cells in area between MA and RP3/4, distally narrowing. Bases of RP3/4 and IR2 are between arculus and nodus, about midway on forewing. Distance between RP3/4 and arculus, 6.5 mm on forewing, on hindwing, 5.7 mm. Exact position of nodus not preserved in the hindwing. Distance between arculus and nodus on forewing, 15 mm. Antenodal area crossed by about twenty or twenty-one antenodal crossveins, not aligned with crossveins between ScP and RA. The two primary antenodal veins are not well preserved, but they were probably similar to the secondary antenodal crossveins. Antenodal area, between ScP and Costa, not widened. Numerous (not less than eight) Bq crossveins in space between IR2, RP and base of RP2. Thirteen crossveins in area between arculus and nodus, between RP and RA. One row of cells in area between RP3/4 and IR2 in its proximal part, distally widened, with five rows of cells in its broadest part, but narrower near posterior wing margin. Nodus very similar to a zygopteroid nodus with costal margin basal of nodus not aligned with costal margin distal of nodus. Oblique nodal vein Cr well aligned with subnodus (fig. 12). Postnodal area very long, with about thirty-nine or forty postnodal veins, some of them being weakly undulated and not aligned with corresponding crossveins between RA and RP1. Base of RP2 very near to subnodus (0.4 mm). One row of cells

in area between RP2 and IR2 on its main part, but distally broadened, with some little branches of RP2 near wing apex. RP2 reaching exactly wing apex. RP2 very straight. A small distinct oblique vein 'O' between RP2 and IR2, two cells distal of subnodus. IR1 base about 12 cells distal of that of RP2. IR1 zigzagged and more or less distally vanishing in area between RP2 and RP1, below pterostigma. Seven rows of cells in broadest part of area between RP2 and RP1, with two small straight secondary longitudinal veins, but distally narrowing near wing apex (only three rows of cells at wing apex). Pterostigma well sclerotised, 3.7 mm long and 1.0 mm wide, covered with small light transverse furrows, covering three cells and not braced. Distance between pterostigma and nodus, 28.7 mm, between pterostigma and apex, 5.2 mm. Post pterostigmal area, between Costa and RA with a secondary zigzagged longitudinal vein.

Genus *Euparasteleopteron* gen. n.

Type species. – *Euparasteleopteron viohli* sp. n.

Etymology. – After the Greek words 'eu' and 'para', and the genus *Steleopteron*.

Diagnosis. – *Euparasteleopteron* is very close to *Parasteleopteron*, the main difference being as follows: (1) no secondary antenodal crossveins between the two primaries; (2) subdiscoidal space with only four crossveins instead of ten; (3) discoidal cell shorter and with two crossveins instead of five; (4) no subdivision of the cells of the area between C and RA distal of pterostigma, except for one or two cells; (5) thirteen secondary antenodal veins instead of sixteen; (6) wing shorter (47.6 mm instead of 55.0 mm long).

Euparasteleopteron viohli sp. n.

(Fig. 15-17)

Material. – Holotype specimen n° SMNS 64432, Staatliches Museum für Naturkunde Stuttgart, Germany. A further (female) specimen of this new taxon is without number in the German private coll. Bürger (Bad Hersfeld). The latter specimen has a wing length of 43 mm and a total body length of 90-91 mm, incl. an ovipositor of 10 mm length. A female specimen without number is in the collection of Dr Kariopp (Regensburg) to be purchased by the Bürgermeister Müller Museum in Solnhofen. It has a wing length of about 48 mm; also an apparent male (!) specimen without number that has a wing length of about 50 mm.

Stratum typicum. – Upper Jurassic, Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

Locus typicus. – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

Etymology. – After Dr Günter Viohl, director of the Jura Museum, Eichstätt.

Diagnosis. – That of the genus.

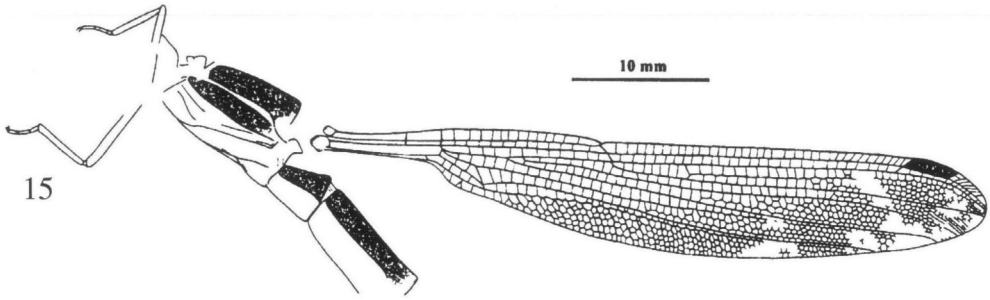
Description (Fig. 15-16). – It is mainly based on the holotype specimen.

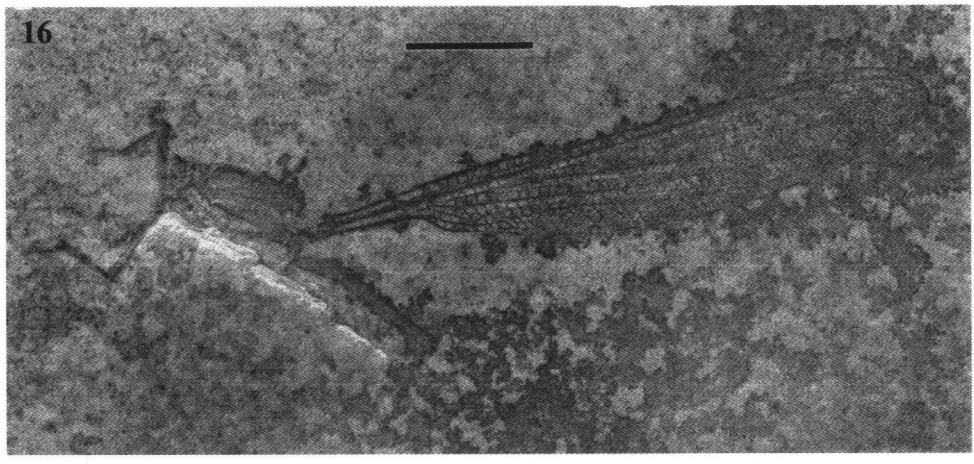
Thorax. Thoracic skewness well pronounced. Angle x, about 50° (sensu Needham & Anthony 1903). Length of thorax, 10.0 mm, width at level of wings' base, about 7.0 mm. Interpleural suture between meso- and metathorax complete (dorsal part present).

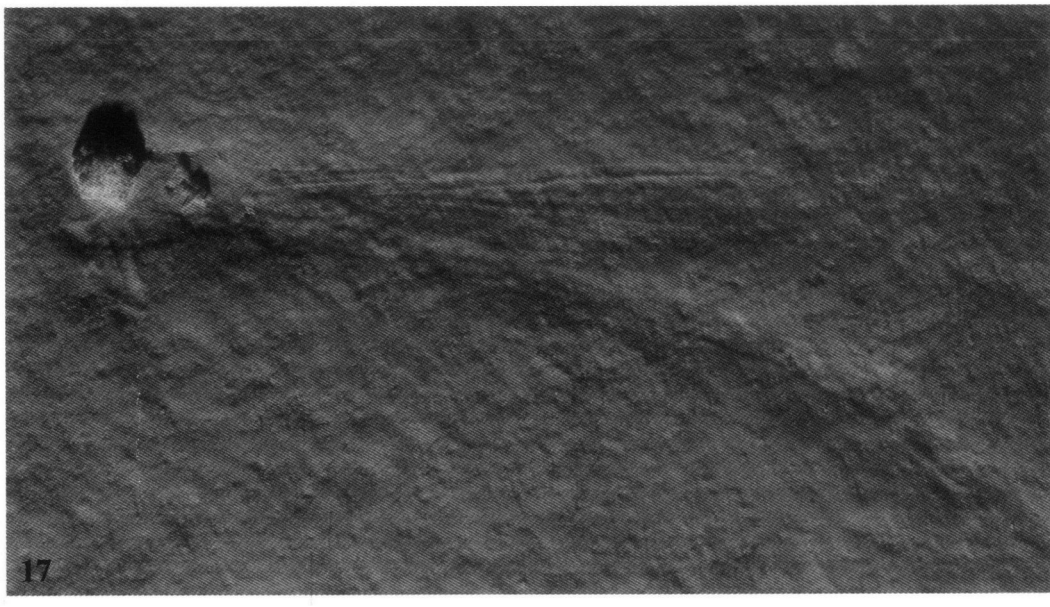
Legs. Two legs preserved. Femora about 7.0 mm long, tibia 4.0 mm long. No spines are visible on the legs, but this could also be due to an artefact of preservation.

Abdomen. Length of first segment, 4.0 mm, of second segment, 8.6 mm. First segment comparatively longer than those of other fossil and modern Odonata, as in other Steleopteridae. There is no secondary genital apparatus visible on the second segment, thus it could be a female specimen, but it could also be an artefact of preservation. Note that the abdomen of the second specimen is very long, as in other Steleopteridae from the Upper Jurassic of Germany.

Wing. Only one wing is preserved. It is impossible to determine whether it is a fore- or a hindwing. Wing 47.6 mm long and 7.3 mm wide; width at the level of the nodus, 6.7 mm. Length of the petiole, about 7.3 mm, width, 2.0 mm. CuP just distal (about 1 mm) separation between AA and AP. AA very straight before reaching CuA, at level of posterior angle of subdiscoidal cell. Arculus at 8.0 mm from wing base; RP separating from MA a little basal of point of contact between RP+MA with posterior part of arculus. Discoidal cells with two crossveins, closed and quadrangular trapezoidal, with distal sides very oblique, not parallel with proximal sides. Length of costal side of discoidal cell, 2.5 mm, of distal side, 1.3 mm, of proximal side, 0.3 mm, of posterior side, 3.6 mm. Subdiscoidal space very long and narrow, crossed by four crossveins. Only one row of cells in cubito-anal area, below subdiscoidal cell. CuA separating from MP at posterior angle of discoidal cell, very short before its fusion with AA. Cubito-anal area gradually widened. CuA strongly zig-







Figures 15. *Euparasteleopteron viohli* gen. and sp. n.: (1) General habitus, holotype specimen SMNS 64432. (16) Photograph, same (scale bar = 10 mm). (17) Photograph, specimen without number in coll. Bürger (without scale, photo by K.A. Frickhinger).

zagged and vanishing distally. One row of cells in area between CuA and MP. Five to six rows of cells in cubito-anal area and in area between MP and posterior wing margin. This area is very long because MP reaches wing margin in distal half of wing, opposite pterostigma, at about 84 % of whole length of wing. No definite branch of MP in area between MP and posterior wing margin. Area between MP and MA proximally broadened near discoidal cell, narrower distally, with one row of cells between MP and MA. MA proximally strong and straight, but distally zigzagged and vanishing in area between MP and RP3/4. MA never reaching posterior wing margin as an independent distinct vein. Only one row of cells in area between MA and RP3/4, distally narrowing. RP3/4 and IR2 branching on RP, about midway between arculus and nodus, on all wings. Distance between RP3/4 and arculus, 4.6 mm. Distance between arculus and nodus, 11.6 mm. Antenodal areas crossed by about thirteen visible antenodal crossveins, not well aligned with crossveins between ScP and RA. Two primary antenodal crossveins preserved, 2.3 mm apart; Ax2 opposite arculus. Antenodal area between ScP and Costa never widened. Six Bq crossveins in area between IR2, RP and base of RP2. Area between arculus and nodus, between RP and RA crossed by eleven crossveins. One row of cells in area between RP3/4 and IR2 in its proximal part, but distally broadened and narrowed near posterior wing margin, opposite pterostigma, with five rows of cells in its broadest part. IR2 straight except near its apex, where it is abruptly curved and vanishing in area between RP3/4 and RP2, opposite pterostigma. Costal margin basal of nodus apparently aligned with costal margin distal of nodus. Nodal vein Cr well-aligned with subnodus. Postnodal area very long, with about thirty six postnodal crossveins, some of them being slightly oblique and not aligned with corresponding crossveins between RA and RP1. Base of RP2 aligned with subnodus. One row of cells in area between RP2 and IR2 in its main part, but it is distally widened, with few small branches of RP2 near wing apex. RP2 reaching exactly wing apex. RP2 very straight. A single (weakly preserved) oblique vein 'O' between RP2 and IR2, two cells distal of subnodus. Base of IR1 about eight cells distal of that of RP2. IR1 zigzagged and more or less distally vanishing in area between RP2 and RP1, at level of pterostigma. Area between RP2 and RP1 wide, six cells wide in its broadest part, without any clear secondary longitudinal veins. It is distally narrowing near wing apex (only two cells wide at wing apex). Pterostigma well defined and sclerotised, 4.0 mm long and 1.0 mm wide. Pterostigma weakly braced, covering four cells. Distance between pterostigma and nodus, 21.3 mm, between pterostigma and apex, 3.3 mm. No secondary zigzagged longitudinal small vein in post pterostigmal area, except for a division of one or two cells.

Genus ***Pseudoeuphaea*** Handlirsch, 1906

(as nomen dubium in Odonata incertae sedis, **sit. n.**)

Type species. – *Pseudoeuphaea areolata* (Hagen, 1862). Other species included (after Handlirsch 1906: 596-597): *P. filosa* (Hagen, 1862), *P. falsificata* Handlirsch, 1906, *P. obscura* Handlirsch, 1906.

Diagnosis. – Handlirsch (1906: 596-597) did not provide any diagnosis of the genus *Pseudoeuphaea*. Since the types of all four species, including the type species, seem to be lost, we consider all these species and the genus *Pseudoeuphaea* as nomina dubia in Odonata incertae sedis.

Pseudoeuphaea areolata (Hagen, 1862)

(as nomen dubium in Odonata incertae sedis, **sit. n.**)

Euphaea areolata Hagen, 1862: 106; Weyenberg, 1869: 235; Meunier 1898: 127.

Pseudoeuphaea areolata: Handlirsch 1906: 596-597 (in Euphaeidae); Calvert 1913: 246; Carpenter 1992: 88 (in family uncertain); Nel & Paicheler 1993: 387 (position discussed); Bridges 1994: VII.18 (list, stated as 'too poorly known to permit assignment to a family').

Pseudoeuphaea Handl. (sic): Fraser 1957: 79 (list, in Euphaeidae).

Holotype. – The type was deposited in the Natural History Museum of Munich, but was probably lost during Second World War.

Stratum typicum. – Upper Jurassic, Malm zeta 2b ('oberer Weißjura'), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

Locus typicus. – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

Taxonomic remarks. – Hagen (1862: 106) only gave the following indications: 'E. areolata Hag. Long. 90 mm; Exp. al. 90 mm. mas. 1 Expl. Eichstätt'. He also added that the holotype was in the Museum of Natural History of Munich. Meunier (1898: 127) redescribed and listed a specimen in the collection of the Museum of Natural History of Munich. He indicated that it is a very badly preserved specimen: 'Une détermination spécifique de

cet insecte n'a aucune valeur scientifique.' Handlirsch (1906: 597) mentioned that there is a specimen Nr. 93 with 50 mm wing length in the Museum of Natural History in Munich, but did not state if this specimen is identical with the type which seems to be unlikely because of the larger size. Anyway, we could not find the specimen(s) in this Museum, so that the type has to be regarded as lost. The statements in the original description concerning the wing length (about 44 mm) and the wing venation (*Lestes*-like cross-venation in the area of the pterostigma) would be compatible with an attribution of this species to *Euparasteleopteron viohli* within Steleopteridae. However, the description is totally insufficient, the specimen was never figured, and the type seems to be lost. Therefore, we have to consider this genus and species as nomina dubia in Odonata incertae sedis.

Pseudoeuphaea filosa (Hagen, 1862)

(as nomen dubium in Odonata incertae sedis, **sit. n.**)

Euphaea filosa Hagen, 1862, 106; Weyenberg 1869: 235; Meunier 1898: 127.

Pseudoeuphaea filosa: Handlirsch 1906: 597 (in Euphaeidae); Calvert 1913: 246; Carpenter 1992: 88 (in family uncertain); Nel & Paicheler 1993: 387 (position discussed); Bridges 1994: VII.86 (list, stated as 'too poorly known to permit assignment to a family').

Pseudoeuphaea Handl. (sic): Fraser 1957: 79 (list, in Euphaeidae).

Holotype. – The type was deposited in the Natural History Museum of Munich, but was probably lost during Second World War.

Stratum typicum. – Upper Jurassic, Malm zeta 2b ('oberer Weißjura'), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

Locus typicus. – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

Taxonomic remarks. – Hagen (1862: 106) only gave the following indications: 'E. filosa Hag. Long. 90 mm; Exp. al. 100 mm. mas. 1 Expl. Eichstätt'. He also added that the holotype was in the Museum of Natural History of Munich. Meunier (1898: 127) redescribed and listed a specimen in the collection of the Museum of Natural History of Munich. He indicated that it is a very badly preserved specimen: 'Tous les caractères étant très effacés, il suffit de dire qu'il est référable au genre *Euphaea*.' Handlirsch (1906: 597) remarked that the correct wing length of this specimen is 53 mm, that the specimen is not well-preserved, and that it could be identical with *P. areolata*. We could not find this specimen in this Museum, thus it seems to be lost as well. This taxon as to be considered as a nomen dubium out of the same reasons that are stated above for *P. areolata*.

Pseudoeuphaea falsificata (Handlirsch, 1906)

(in Odonata incertae sedis, **sit. n.**)

'*Euphaea longiventris* Hagen, 1862': Meunier 1898: 127, pl. 26, fig. 81-82 (figured specimen).

?*Pseudoeuphaea falsificata* Handlirsch, 1906: 597 (in Euphaeidae).

Pseudoeuphaea falsificata: Calvert 1913: 246 ; Carpenter 1992: 88 (in family uncertain); Nel & Paicheler 1993: 387 (position discussed); Bridges 1994: VII.83 (list, stated as 'too poorly known to permit assignment to a family').

Pseudoeuphaea: Fraser 1957: 79 (list, in Euphaeidae).

Holotype. – The type was in the Museum of Natural History of Munich but it is probably lost.

Stratum typicum. – Upper Jurassic, Malm zeta 2b ('oberer Weißjura'), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

Locus typicus. – Eichstätt / Solnhofen?, southern Frankonian Alb, Bavaria, Germany.

Taxonomic remarks. – '*Euphaea longiventris*' (sensu Hagen 1862: 106, 121, pl. 13, fig. 7-8) has been synonymised with *Tarsophlebia eximia* Hagen, 1862 by Handlirsch (1906: 580) in 'Anisozygoptera' Tarsophlebiidae. The holotype of '*Euphaea longiventris*' was figured under the name of *Tarsophlebia eximia* by Malz & Schröder (1979: 27, fig. 14) and is deposited as specimen n° SMF VI 50a at the Senckenberg Museum in Frankfurt. One of the authors (G.B.) recently examined the type of Hagen (wing length, 35 mm) and could definitely confirm the opinion of Handlirsch (1906: 580) that it is a synonym of *Tarsophlebia eximia*.

Handlirsch (1906: 597) indicated that the specimen figured by Meunier (1898: pl. 26, fig. 81-82) does not belong to '*Euphaea longiventris*'. Later, Calvert (1913: 252) has erroneously considered that this specimen would belong to '*Euphaea longiventris*' and not to a different species, but the same author (p. 246) also indicated that Handlirsch (1906) has described 'four possible, but indecipherable species of *Pseudoeuphaea*'. *Pseudoeuphaea falsificata* is one of those species, its type-specimen is the one that Calvert has considered to belong to '*Euphaea longiventris*'.

The type-specimen of *Pseudoeuphaea falsificata* is figured (photograph of the part and counterpart) by Meunier under the name *Euphaea longiventris*, but, in Meunier's (1898: 127) complete list of the fossil insects of the same collection, there is no specimen that would correspond to the photograph, except the specimen that Meunier has labelled '*Euphaea multinervis*' (part and counterpart). The only listed specimens by Meunier under the name '*Euphaea longiventris*' are two isolated wings and a specimen with the wings in a very different position. The specimen figured by Meunier (1898: pl. 26, fig. 81-82) is nearly but not exactly in the same position as the holotype of '*Euphaea multinervis*' given by Hagen (1862: pl. 14, fig. 2). The only solution of this curious problem is that the legend of Meunier's figures 81-82 is erroneous, and Meunier (1898) probably did consider that these figures being those of a specimen of '*Euphaea multinervis*' (= *Euphaeopsis multinervis*). This specimen would need a revision to determine if this is true.

Pseudoeuphaea obscura (Handlirsch, 1906)

(as nomen dubium in Odonata incertae sedis, **sit. n.**)

'ailes d'*Euphaea*' and '*Euphaea longiventris*, Hagen'; Meunier 1898: 127, pl. 8, fig. 14.
?*Pseudoeuphaea obscura* Handlirsch, 1906: 597 (in Euphaeidae).
Pseudoeuphaea obscura: Calvert 1913 : 246 ; Carpenter 1992: 88 (in family uncertain); Nel & Paicheler 1993: 387 (position discussed); Bridges 1994: VII.169 (list, stated as 'too poorly known to permit assignment to a family').
Pseudoeuphaea: Fraser 1957: 79 (list, in Euphaeidae).

Holotype. – The type was deposited in the Natural History Museum of Munich, but was probably lost during Second World War, since we could not find this specimen in this museum.

Stratum typicum. – Upper Jurassic, Malm zeta 2b ('oberer Weißjura'), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

Locus typicus. – Eichstätt / Solnhofen?, southern Frankonian Alb, Bavaria, Germany.

Taxonomic remarks. – Handlirsch (1906: 597) mentioned that the type shows two isolated wings (length, about 37 mm) on the same plate of lithographic limestone, which have a very long petiole and numerous intercalary veins. Unfortunately, this taxon as to be considered as a nomen dubium out of the same reasons that are stated above for *P. areolata*.

Genus ***Euphaeopsis*** Handlirsch, 1906

(*in* Epiproctophora: Isophlebioidea (Isophlebiidae or Campterophlebiidae) **sit. n.**)

Type species. – *Euphaeopsis multinervis* (Hagen, 1862), by monotypy.

Diagnosis. – Handlirsch (1906) did not provide any diagnosis of this genus. We here provide a diagnosis which is based on our redescription below: (1) fore- and hindwing discoidal cells closed and elongate; (2) numerous secondary antenodal crossveins between ScP and C; (3) postdiscoidal area narrow, narrower near posterior wing margin than near discoidal cell; (4) subdiscoidal space larger than discoidal cell, but posteriorly closed; (5) AA never fused with CuA; (6) two rows of cells in cubital area and CuA with no posterior branches; (7) wing length ranging between 50 mm and 62 mm. This species is distinctly smaller than the two 'giant' isophlebiid *Isophlebia aspasia* Hagen, 1866 and *Anisophlebia helle* (Hagen, 1862) from the same outcrops.

Euphaeopsis multinervis (Hagen, 1862)

(Fig. 18-20)

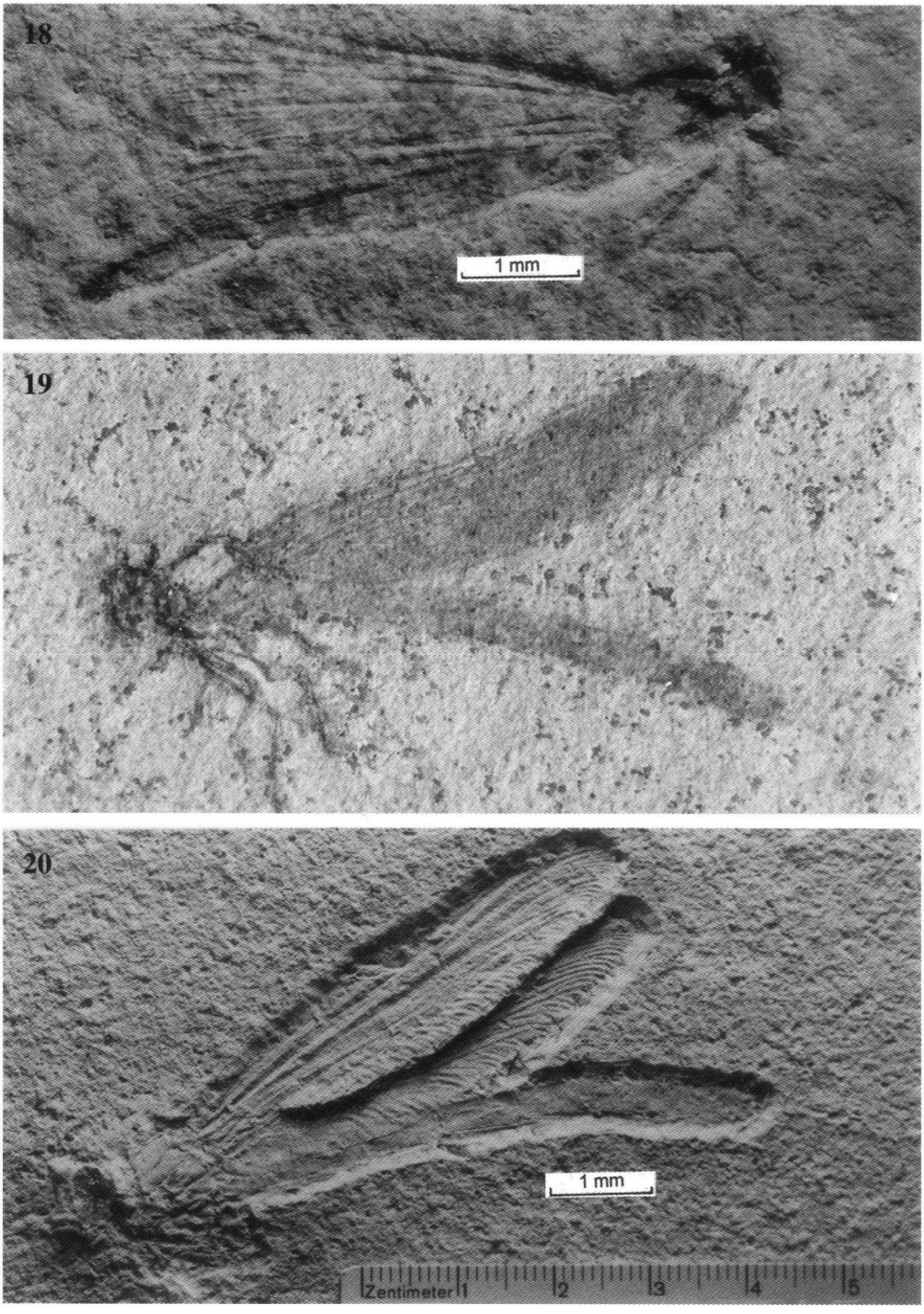
Euphaea multinervis Hagen, 1862: 106, 119-121, pl. 14, fig. 2-4.
Euphaeopsis multinervis: Handlirsch 1906: 596, pl. 47, fig. 19 (in Euphaeidae); Calvert 1913: 246, 248, 252-254 (in Euphaeidae); Carpenter 1992: 88 (in family uncertain); Nel & Paicheler 1993: 387 (position discussed); Bridges 1994: VII.160 (list, stated as 'too poorly known to permit assignment to a family').
Euphaeopsis Handl. (sic): Fraser 1957: 79 (list, in Euphaeidae).

Note. – Lakshminarayana & Kumar (1988) named, without any description or figure, *Euphaeopsis hageni*. Nel & Paicheler (1993) indicated that this is a nomen nudum.

Holotype. – Hagen (1862: 106) mentioned two specimens of this species in the collection of the Natural History Museum in Munich: 'E. multinervis Hag. Long. 70 mm; Exp. al. 100 mm. fem. 2 Expl. Eichstätt'. However, in the same work (Hagen 1862: 119-121, pl. XIV, Fig. 2-4) he only describes and figures a single specimen, which therefore has to be considered as the holotype of this species. Meunier (1898: 127) added that the part and counterpart of a specimen from the 'Leuchtenberg'sche Sammlung' was in the Museum of Natural History of Munich, and Handlirsch (1906) indicated the presence of a specimen (n° 90) in the Museum of Natural History of Munich as well. Consequently, the type specimen should be expected in the Museum of Natural History in Munich, but we could not find either of the two specimens there. However, one of the authors (G.B.) recently rediscovered the part and counterpart of this holotype in the collection of the Senckenberg Museum in Frankfurt, with the specimen number SMF VI 45a,b. It is labelled 'Euphaeopsis multinervis; Typus; Tf. 14, Fig. 2-4; Nachlass H. v. Meyer'. The body, wing length and all visible characters of this specimen correspond to the description of Hagen (1862), and the general appearance of this fossil shows that it is without doubt the same specimen that was figured by Hagen (1862: pl. 14, fig. 2). Since there is a secondary genital apparatus visible, this holotype is a male specimen.

Further material. – Specimen without number at MCZ, Cambridge, USA (labelled as 'Agrionin, coll. Haeberlein, Solenhofen') (Fig. 25); specimen n° SOS 4654 at JME, Eichstätt, Germany (labelled as 'Odonata sp., Schernfeld, Schäfer 1998') (Fig. 24) which was also figured by Frickhinger (1999: fig. 102) as 'undetermined dragonfly in coll. Schäfer, Nürnberg'; a further specimen without number that obviously belong to this species has also been figured in Frickhinger (1999: fig. 98) as 'undermined dragonfly' from a German private collection (coll. Kariopp, Regensburg).

Remarks. – Two other specimens figured in the same work (Frickhinger 1999: fig. 99 of a specimen with 5.5 cm wing length in coll. Bürger / Bad Hersfeld, and fig. 100 of a specimen with 35 mm wing length in coll. Kümpel / Wuppertal) are similar in the general habitus, but differ significantly in wing venation and size. The specimen in coll. Kümpel was studied by one of the



Figures 18-20. Photographs, *Eupnaeopsis multinervis* (Hagen, 1862): (18) Holotype specimen SMF VI 45b (part). (19) Specimen SOS 4654, (without scale, photo by K.A. Frickhinger). (20) Specimen without number at MCZ.

authors (G.B.) and indeed has a wing length of only 28 mm and a body length of 44 mm. Therefore, both specimens seem to belong to different new taxa, and do not seem to be Steleopteridae at all.

Stratum typicum. – Upper Jurassic, Malm zeta 2b ('oberer Weißjura'), Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

Locus typicus. – Eichstätt / Solnhofen, southern Frankonian Alb, Bavaria, Germany.

Redescription. – The redescription and figure of Handlirsch (1906) are very incomplete, not precise and contains several errors, so that a redescription is necessary.

(A) Specimen SOS 4654. A nearly complete specimen with at least a fore- and hindwing in connection to the body. As the wings are superposed, it is very difficult to check the wing characters. The main part of the forewing is hidden under the hindwing, forewing 62 mm long, width unknown; distance between base and nodus, about 25 mm, between nodus and apex, about 37 mm, thus the nodus is in a proximal position; pterostigma not visible; secondary antenodal crossveins of first and second rows numerous. Hindwing 58 mm long and about 9 mm wide; distance between base and nodus, 20.5 mm, between nodus and apex, about 37.5 mm, thus the nodus is in a proximal position; pterostigma long and broad, 5.5 mm long and 1.0 mm wide, rather basally recessed, 6.7 mm from wing apex; pterostigmal brace not preserved; arculus oblique as in other Isophlebiidae; discoidal cell quadrangular, long and narrow, 2.5 mm long and 0.6 mm wide, apparently free of crossveins; basal part of CuA (cubital gaff sensu Bechly 1996) strong and rather long, 1.0 mm long; area between CuA and MP broader than postdiscoidal area between MA and MP, 1.5 mm instead of 1.2 mm wide; subdiscoidal space broad, 1.5 mm long and 1.2 mm wide; AA never reaching CuA, but the posterior wing margin; anal area broad, 1.6 mm wide; anal wing margin rounded (probably a female specimen, also probable because of the apparent absence of secondary genital apparatus on second abdominal segment); secondary antenodal crossveins of first and second rows numerous; postnodal crossveins of both first and second rows numerous; CuA distally zigzagged and vanishing in area between MP and posterior wing margin, well basal of nodus, with no clear secondary branches; cubital area with two rows of cells between CuA and posterior wing margin; MP slightly undulate, reaching posterior wing margin well distal of nodus; postdiscoidal area with only one row of cells, and distally narrowed; base of RP3/4 3.2 mm distal of arculus, closer to arculus than to nodus; base of IR2 8.1 mm distal of arculus, five cells distal of base of RP3/4; MA nearly straight; RP3/4 slightly undulate; oblique vein 'O' not visible. Head very poorly preserved and useless. Thorax strong, 7.0 mm high and 9.5 mm long; angle x, 32° thus thoracic skewness sensu Needham & Anthony (1903) similar to that of the Anisoptera and Isophlebioidea (Fleck & Nel in prep.); presence of a complete interpleural suture, as in Isophlebioidea (Fleck & Nel in prep.); abdomen strong, about 56 mm long and 5 mm wide; abdominal carinae not preserved, if present; cerci and genital appendages not clearly preserved.

(B) Specimen without number at MCZ, Cambridge, USA. A nearly complete specimen but with the forewing partly overlapping the hindwing. The dimensions are similar and the preserved wing venation structures are identical to those of specimen SOS 4654. The forewing discoidal cell is closed and quadrangular elongated but shorter than the hindwing one. Forewing length, about 56 mm; hindwing length, about 52 mm, abdomen, 57 mm long; abdomen and thorax strong; presence of the longitudinal ventral carina of the abdominal tergites and of a complete thoracic interpleural suture.

(C) Specimen SMF VI 45a,b (holotype). Part and counterpart of a body with the wings in connection, fossilised in the same position as the two other specimens, but more poorly preserved. The wing venation is nearly indecipherable but the dimensions are similar to those of the other specimens. Forewing length, more than 47 mm; hindwing length, more than 47 mm, abdomen, about 50 mm long. Vein MA is straight, postdiscoidal area very narrow, MP slightly undulate and very long; numerous antenodal crossveins.

Discussion. – The wing lengths of these three specimens, ranging between 50 mm and 62 mm, are compatible with intraspecific variations. Furthermore, there is no preserved character that would justify a specific separation.

After the present redescription, *Euphaeopsis multinervis* shares with the Isophlebioidea the following characters: (1) a broad area between MP and CuA, broader than postdiscoidal area; (2) postdiscoidal area very narrow, distally narrower;

(3) cubital gaff long and strong; (4) hindwing subdiscoidal space transverse, long and broad, larger than discoidal cell; (5) AA not reaching CuA; (6) numerous secondary antenodal crossveins between ScP and C; (7) forewing discoidal cell closed and elongated, similar to the hindwing one; (8) MP only slightly undulate and MA straight.

Characters (1), (3), (4) and (5) are synapomorphies of Isophlebioidea (= Campterophlebiidae + Isophlebiidae). Character (2) is a unique synapomorphy of the Campterophlebiidae (Bechly 1996), but character (7), considered as a synapomorphy of Isophlebiidae by the same author, would contradict the attribution of *E. multinervis* to the Campterophlebiidae. Nevertheless, this character is highly homoplastic within the Odonata. Character (6) is present in Isophlebiidae (no secondary antenodal crossveins between ScP and C in Campterophlebiidae), but its polarity remains uncertain. In conclusion, the exact attribution of *Euphaeopsis* to the Campterophlebiidae or to the Isophlebiidae remains uncertain. We prefer to consider it as a Isophlebioidea incertae sedis.

Palaeoecological considerations

The very long ovipositor of the Steleopteridae is superficially 'similar' to the hypertrophied ovipositor of the extant Cordulegastridae (Nel & Martínez-Delclòs 1993), and the fossil Aeschnidiidae and Tarsophlebiidae (Nel et al. 1993). This organ probably was not suited for endophytic oviposition. Female Steleopteridae could have deposited the eggs in mud and sand, just like modern Cordulegastridae, and used its ovipositor to make holes in the mud (d-type of 'flying-oviposition into mud or sand' sensu Eda 1960 or Inoue & Shimizu 1976). Nevertheless, the cordulegastrid ovipositor is straight, clearly shorter, and more apically rounded than that of the Steleopteridae. The cordulegastrid tenth segment is small (diameter inferior to the ninth), and in dorsal position, unlike that of the Steleopteridae. The probable presence of muscles in the last abdominal segments (see above), related to the ovipositor, together with the long tenth segment and the curved ovipositor, suggests that the steleopterid ovipositor may have had a different function to those of all extant Odonata, maybe for a egg-laying in holes or plant or fungal cavities. The tarsophlebiid ovipositor is very similar in size and shape to that of the Steleopteridae (long and curved) and could have had a similar function. Nevertheless, the Tarsophlebiidae have a shorter abdomen relative to the wing length, and very long and slender legs, unlike the Steleopteridae (Nel et al. 1993). Therefore, they probably did not have the same biology.

Similar to the Pseudostigmatidae and Perilestidae, which are the only extant Odonata with a comparatively elongated abdomen and relatively small pterothorax, the Steleopteridae probably have not been very good fliers. They may have lived as cryptic animals in areas with dense vegetation, e.g. gallery forests.

Phylogenetic affinities of the Steleopteridae

Bechly (1996) tentatively attributed the Steleopteridae to the Epiproctophora (sensu Bechly 1996) because of the following characters, but did not exclude a position within Zygoptera close to basal Caloptera like Sieblosiidae:

(1) Arculus shifted basally in a position between the two primary antenodals Ax1 and Ax2 (synapomorphy of all Epiproctophora). However, Bechly (1999) already mentioned that this character would need further confirmation. Our present study showed that the only Steleopteridae with the primary antenodals well preserved are specimen PIN 2904/8 (attributed herein to *Auliella crucigera*) and the holotype of *Euparasteleopteron viohli*. The former clearly has the arculus in a distal position relative to Ax2, while the latter has the arculus aligned with Ax2. The relative position of Ax2 and the arculus is unknown in the other steleopterids.
(2) Presence of the lestine-oblique-vein 'O' (mentioned by Bechly as a shared plesiomorphy).
(3) Position of RP3/4 and IR2 midway between nodus and arculus. As already stated by Bechly (1996), this character is shared by Epiproctophora, but is also present in several clades within the Zygoptera (Sieblosiidae, Lestoidea). Thus, this character is at least very homoplastic.

The members of Epiproctophora also share the following synapomorphies:

(4) Distinct anal angle in male hindwing. No male steleopterid has been described yet.
(5) Costal margin not indented at node. In the type specimens of *Auliella*, *Parasteleopteron*, and *Euparasteleopteron* the costal margin is indented at the nodus. The costal margin of the type specimen of *Steleopteron* is too poorly preserved for an accurate conclusion about this character. Consequently, the Steleopteridae do not share this apomorphy with the Epiproctophora.
(6) Suppression of the zygopteroid paired appendix inferior and development of secondary epiproctal projection (in males). This character is unknown in Steleopteridae.

(7) Thorax and abdomen relatively strong and stout. The Steleopteridae indeed have a relatively robust, even though very elongated, abdomen, but they have a very gracile pterothorax.
(8) Posterior tergal sclerite of the metathorax suppressed and the anterior sclerite enlarged. This character is unknown in Steleopteridae.
(9) Adult synthorax with the dorsal portion of the interpleural suture suppressed. Bechly (1996) did not give an 'outgroup' argument to polarise this character, but of course a complete suture between two separate segments has to be considered as plesiomorphy anyway. We could observe on two undescribed Protozygoptera (sister group of the Panodonata) from the Permian of Russia (specimens PIN 1700/456 and PIN 1700/4655) the presence of a complete interpleural suture. In *Parasteleopteron* and *Euparasteleopteron*, this suture is clearly present at least in its dorsal portion. Please note that this character in fact does not seem to be a groundplan apomorphy of the Epiproctophora, since a still undescribed genuine Isophlebioidea also has retained a complete suture (Fleck et al. submitted).

In conclusion, the arguments proposed by Bechly (1996) for the attribution of Steleopteridae to Epiproctophora have to be considered as obsolete, since there are no convincing synapomorphies. The Steleopteridae only share with the Epiproctophora:

(1) Presence of a ventro-lateral longitudinal carina on the abdominal tergites (character of uncertain polarity);
(2) Absence of a longitudinal carina on the abdominal sternites (maybe a symplesiomorphy);
(3) The pterostigma is covered with weak transverse furrows (maybe a symplesiomorphy as well).

These structures are known in nearly all Anisoptera, Epiophlebiidae, Heterophlebioidea, and undescribed Isophlebioidea (Nel et al. 1993; Fleck & Nel in prep.).

Even though Bechly (1996) considered the presence of a longitudinal ventral carina on the abdominal sternites as a zygopteroid autapomorphy, the polarity of this character within Odonata (= Zygoptera + Epiproctophora) still has to be considered as somewhat uncertain, because it is unknown in more basal groups sensu Bechly (1996), i.e. (Tarsophlebioidea, Protozygoptera, Triadophlebioptera, and Protanisoptera).

The Steleopteridae share with the Zygoptera the following putative synapomorphies sensu Bechly (1996):

(1) Both fore- and hindwing well petiolated, with a petiole distinctly longer than wide.
(2) Both pairs of wings of identical shape and venation (?). The differences between the fore- and hindwing (dimensions of the pterostigma and discoidal cell), present in the Steleopteridae, also occur in some modern Zygoptera (*Sympecma fusca*, among others), even though probably as a reversal.
(3) Head transverse, very elongated and medially compressed. The head is possibly present in the holotype of *Steleopteron*. If it is so, it would be transverse and elongated.
(4) Thorax and abdomen rather gracile, and the abdomen is very long. The thorax of Steleopteridae is gracile indeed, and the abdomen is strongly elongated, but still robust.
(5) A very extreme obliquity of the pterothorax (thoracic skewness sensu Needham & Anthony 1903). Bechly (1996) could not yet provide an 'outgroup' argument to support the polarity of this character. Fortunately, we had the opportunity to determine the thoracic skewness of two undescribed Protozygoptera (sister group of the Panodonata) from the Permian of Russia (specimens PIN 1700/456 and PIN 1700/4655). Their angle x ranges between 35° and 40° and their thorax are large and broad, more looking like the thorax of the Isophlebioidea, the Epiophlebiidae and the Anisoptera. The Steleopteridae clearly share the apomorphic zygopteroid character state.

Other zygopteroid synapomorphies proposed by Bechly (1996) are unknown in Steleopteridae. Nevertheless, the Steleopteridae share five putative synapomorphies with the Zygoptera, but no known synapomorphy with the Epiproctophora, with the possible exception of the presence of a ventro-lateral abdominal tergal carina which of course still is of uncertain polarity. Therefore, we propose to exclude the Steleopteridae from the Epiproctophora and retransfer them to Zygoptera.

Bechly (1996) divided the Zygoptera into Caloptera and Euzygoptera. The Caloptera (= fossil Triassolestidae + fossil Sieblosiidae + modern Eucaloptera according to Bechly 1996, but Bechly 1997 excluded the Triassolestidae from the Caloptera and transferred them into the Epiproctophora - Isophlebioptera - Parazygoptera) are characterised by the following synapomorphies, that appear to be relatively weak (therefore, Bechly (1996) also discussed an alternative hypothesis of a sistergroup relationship of Caloptera and Coenagrionomorpha):

(1) Midfork (bases of RP3/4 and IR2) recessed basally to a position between 12-26 % of wing length. These veins are distal of the nodus in Protozygoptera and at about 30 % in *Tarsophlebia eximia* Hagen, 1862 but at 26 % in *Turanophlebia martynovi* Pritykina, 1968 and at 21 % in *Euthemis cellulata* Pritykina, 1968 (Tarsophlebioidea, sister group of Odonata sensu Bechly 1996). Thus the polarity of this character is uncertain. Furthermore, this character is indeed of relatively weak value, because it is convergent with the Euzygoptera: Lestinoidea and Hypolestinae (as

indicated by Bechly 1996), but also in the Coenagrionomorpha: Pseudostigmatidae (*Pseudostigma* sp.). In Steleopteridae, the midfork is at 23-29 % of the wing length (in *Parasteleopteron* and *Steleopteron*), probably because of the very long petiole.

(2) Stigmal vein brace obsolete. In many Euzygoptera, the stigmal brace is also obsolete (*Heteragrion* sp., *Philogenia* sp., *Argiolestes* sp., *Hemiphlebia mirabilis*, *Isosticta* sp., *Pseudostigma* sp., etc.). Thus, at least, this character is highly homoplastic. In most Steleopteridae (except *Euparasteleopteron*), it is distinctly reduced, but still visible.

(3) The basal closure of discoidal cell, which is of weak value since it is also present as multiple convergence in many Euzygoptera and Epiproctophora.

Bechly (1996) listed the following putative synapomorphies for the Eucaloptera :

(1) Tendency towards a more or less rectangular discoidal cell. Bechly (1996) supposed that this character is 'reversed in Amphipterygidae and many Chlorocyphoidea?' In more basal groups, such as the Protozygoptera, there is an acute angle between vein MAb and MP (+ CuA), thus the polarity of this character state proposed by Bechly is possible. In Steleopteridae, MAb is very oblique and the discoidal cell looks like those of the Amphipterygidae. It is one of the reasons proposed by Fraser (1957) to synonymise the two families.

(2) Very oblique basal margin of the pterostigma. This apparently strong synapomorphy of the Eucaloptera is absent in Steleopteridae, but the pterostigma is absent in many Calopterygidae, and the basal margin is not oblique in the male *Hetaerina caja* and male *H. americana*.

(3) Lestine oblique vein 'O' reduced. It is not so in Steleopteridae.

Therefore, the Steleopteridae share none of the 'usable' synapomorphies of the Eucaloptera, thus there is no evidence for their inclusion in this group.

Bechly (1996) listed the following putative synapomorphies for the Euzygoptera:

(1) Longitudinal veins rather straight and long. In Steleopteridae, some of these veins are straight and long (RP3/4 and IR2) but others are distally vanishing. Thus, the character is ambiguous in this group.

(2) One (or two, in some Lestidae, at least) row of cells between CuA and posterior wing margin. This character is present in Steleopteridae, but it is probably related to the extreme elongation of these wings.

(3) Only the two primary antenodals retained. The polarity of this character remains somewhat ambiguous, because in Tarsophlebioidea there are numerous secondary antenodals, while in Protozygoptera there are frequently only the two primaries retained (convergence?). In Steleopteridae, there are numerous secondary antenodal crossveins.

(4) Antesubnodal space without any crossveins. It is not so in Steleopteridae.

(5) No crossveins present in the space between RP and MA basal of midfork. This homoplastic character is not present in Steleopteridae.

Consequently, the Steleopteridae share no strong synapomorphies with either Caloptera, or Euzygoptera. Thus, it is not possible to propose any attribution of this family to one of these two taxa within crowngroup Zygoptera. We currently prefer to consider the Steleopteridae as Zygoptera of uncertain affinities. Because of the several possible plesiomorphic character states (pterothoracic interpleural suture complete, presence of the ventro-lateral longitudinal carina on the abdominal tergites, absence of the longitudinal carina of sternites, pterostigma covered with light transverse furrows, discoidal cells of different shape in fore- and hindwings), partly shared with the Epiproctophora, the Steleopteridae seem to be in a very basal position within Zygoptera, and therefore could rather belong to the stemgroup than to the crowngroup of Zygoptera.

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