Günter BECHLY[1]

NEW FOSSIL ODONATES FROM THE UPPER TRIASSIC OF ITALY, WITH A REDESCRIPTION OF *ITALOPHLEBIA GERVASUTTII* WHALLEY, AND A RECLASSIFICATION OF TRIASSIC DRAGONFLIES (INSECTA: ODONATA)

RIASSUNTO: In questo lavoro viene revisionata la fauna ad odonati del Triassico Superiore della Bergamasca. Sono descritti il primo Protomyrmeleontidae del Triassico europeo: *Italomyrmeleon bergomensis* gen. e spec. nov. e un minuscolo odonato fossile (nuovo genere e nuova specie) a cui non viene attribuito un nuovo nome per la sua scarsa conservazione. Viene ridescritta *Italophlebia gervasuttii* e si descrive una nuova specie appartenente allo stesso genere, *Italophlebia paganoniae* spec. nov. Si discute la posizione filetica di *Italophlebia,* si dimostra che si tratta di uno dei più antichi rappresentanti di Anisoptera; viene perciò trasferito da Zygoptera - Hemiphlebioidea a „Anisozygoptera" - Isophlebioptera. In Isophlebioptera viene proposto il nuovo "clade" Parazygoptera, viene inoltre introdotto il sistema filogenetico nei suoi sottogruppi. Italophlebiidae è considerato come un sinonimo di Triassothemistini, Progonophlebiidae come sinonimo di Mesophlebiinae. Triassoneuridae è considerato sinonimo di Triassolestidae, Oreopteridae come sinonimo di Asiopteridae. Viene proposto il nuovo genere *Pseudotriassothemis* gen. nov. (genere tipo di Pseudotriassothemistinae subfam. nov.) basato su tre specie del Triassico giapponese: „*Triassoneura*" okafujii, „*Triassothemis*" nipponensis e „*Triassothemis*" minensis. è proposto il nuovo sottogenere di *Triassothemis, Afrotriassothemis* subgen. nov., per le due specie Triassiche del Sud Africa *T. heidiae* e *T. regularis,* queste erano state precedentemente classificate nel genere *Triassoneura.* „*Triassoneura*" primitiva viene trasferita da Triassoneuridae a Archizygoptera - Batkeniidae in un nuovo genere *Paratriassoneura* gen nov. La specie „*Sogdopteron*" legibile viene trasferita da Asiopteridae a Triassolestini. *Sogjutella mollis* è trasferita da Asiopteridae a Cyclothemistidae. *Sphenophlebia, Mesoepiophlebia* e *Ensphingophlebia* vengono trasferite da Euthemistidae e Epiophlebiidae nella nuova famiglia Sphenophlebiidae fam. nov. che è considerato il gruppo più basale di Parazygoptera. Ad un esame preliminare anche *Proeuthemis pritykinae* viene trasferita da Euthemistidae alla nuova famiglia Sphenophlebiidae, sebbene possa anche essere anche un "sister-group" di Asiopteridae. Si trasferisce „*Sphenophlebia*" pommerana al genere *Turanopteron* in Asiopteridae. *Triadotypus guillaumei* viene riconosciuto come un sinonimo di *Reisia gelasii,* viene inoltre descritta *Reisia nana* spec. nov., proveniente dal Triassico della Francia. *Triadotypus sogdianus* viene quindi cambiato in *Reisia sogdianus* comb. nov. *Reisia* (= *Triadotypus*) e *Triassologus* sono entrambe trasferite da „Protodonata" in

[1] Institute and Museum of Geology and Paleontology, Eberhard-Karls University, Tübingen, Germany

Triadophlebioptera; pertanto non sono più riconosciuti protoodonati Triassici. *Thuringopteryx gimmi* viene trasferito da „Protodonata" a Palaeodictyoptera, costituendo il primo rappresentante Triassico di questo gruppo.

SUMMARY: The odonate fauna of the Upper Triassic of Bergamo is revised. *Italomyrmeleon bergomensis* gen. et spec. nov. is described as first Protomyrmeleontidae from the Triassic of Europe. A tiny fossil odonate which belongs to a new genus and species is described but not named because it is a poorly preserved specimen. *Italophlebia gervasuttii* is redescribed and a new species of the same genus, *Italophlebia paganoniae* spec. nov., is described. The phylogenetic position of *Italophlebia* is discussed and the genus is shown to be one of the oldest known stem-group representatives of Anisoptera, and is therefore transferred from Zygoptera - Hemiphlebioidea to „Anisozygoptera" - Isophlebioptera. Within Isophlebioptera a new clade Parazygoptera is proposed and a phylogenetic system of its subgroups is introduced. Italophlebiidae is regarded as junior subjective synonym of Triassothemistini stat. nov., and Progonophlebiidae is regarded as junior subjective synonym of Mesophlebiinae. Triassoneuridae is regarded as junior subjective synonym of Triassolestidae, and Oreopteridae is regarded as junior subjective synonym of Asiopteridae. A new genus *Pseudotriassothemis* gen. nov. (type genus of Pseudotriassothemistinae subfam. nov.) is erected for the three Japanese Triassic species „*Triassoneura*" *okafujii*, „*Triassothemis*" *nipponensis* and „*Triassothemis*" *minensis*. *Afrotriassothemis* subgen. nov. is proposed as new subgenus in *Triassothemis* for the two South African Triassic species *T. heidiae* and *T. regularis*, that were previously classified in the genus *Triassoneura*. „*Triassoneura*" *primitiva* is transferred from Triassoneuridae to Archizygoptera - Batkeniidae in a new genus *Paratriassoneura* gen nov. „*Sogdopteron*" *legibile* is transferred from Asiopteridae to Triassolestini. *Sogjutella mollis* is transferred from Asiopteridae to Cyclothemistidae. *Sphenophlebia*, *Mesoepiophlebia* and *Ensphingophlebia* are transferred from Euthemistidae and Epiophlebiidae to a new family Sphenophlebiidae fam. nov. which is regarded as most basal group of Parazygoptera. *Proeuthemis pritykinae* is preliminarily transferred from Euthemistidae to the new family Sphenophlebiidae too, although it might also be the sister-group of Asiopteridae. „*Sphenophlebia*" *pommerana* is transferred to the genus *Turanopteron* in Asiopteridae. *Triadotypus guillaumei* is recognised as junior subjective synonym of *Reisia gelasii* and *Reisia nana* spec. nov. is described from the Triassic of France. Consequently *Triadotypus sogdianus* is changed to *Reisia sogdianus* comb. nov. *Reisia* (= *Triadotypus*) and *Triassologus* are both transferred from „Protodonata" to Triadophlebioptera, so that there are no Triassic protodonates known any longer. *Thuringopteryx gimmi* is transferred from „Protodonata" to Palaeodictyoptera, as the first known Triassic representative of this group.

PAROLE   CHIAVE: Insecta, Palaeodictyoptera, „Protodonata", Odonata, Archizygoptera, Protomyrmeleontidae, Zygoptera, Hemiphlebioidea, „Anisozygoptera", Oreopteridae, Asiopteridae, Cyclothemistidae, Mesophlebiidae, Progonophlebiidae,

Triassolestidae, Triassoneuridae, Triassothemistidae, Italophlebiidae, subfam. nov., gen. nov., subgen. nov., spec. nov., „Anisozygoptera" - Isophlebioptera, nuova sinonimia, tassonomia, filogenesi, cladistica, fossile, Triassico, Italia, Bergamo.

KEY WORDS: Insecta, Palaeodictyoptera, „Protodonata", Odonata, Archizygoptera, Protomyrmeleontidae, Zygoptera, Hemiphlebioidea, „Anisozygoptera", Oreopteridae, Asiopteridae, Cyclothemistidae, Mesophlebiidae, Progonophlebiidae, Triassolestidae, Triassoneuridae, Triassothemistidae, Italophlebiidae, subfam. nov., gen. nov., subgen. nov., spec. nov., new synonymy, taxonomy, phylogeny, cladistics, fossil, Triassic, Italy, Bergamo.

INTRODUCTION. Fossil dragonflies from the Triassic are of particular interest since they have retained a lot of plesiomorphic characters and represent rather basal stem-group representatives of recent higher taxa, and thus provide new insights into the evolution of these groups. While in Handlirsch's (1906-1908) „bible" of paleoentomology there were still no Triassic odonates mentioned at all, meanwhile several localities fortunately provided very interesting material (see below). The first and until now sole description of fossil insects from the Upper Triassic of Italy has been given by Whalley (1986), who also described *Italophlebia gervasuttii* after five odonate specimens in the collection of the Museo Civico di Scienze Naturali in Bergamo. In the meantime further specimens have been discovered and I had the opportunity to study all this material during a visit in Bergamo in September 1996. On occasion of this visit I could identify the first female specimen of *Italophlebia gervasuttii* and also three new odonate species. The new specimens have been collected by Matteo Malzanni during field researches in the Argilliti di Riva di Solto with financial support by the city of Bergamo.
The specimen that was designated by Whalley (1986) as paratype of *Italophlebia gervasuttii* turned out to represent a new genus and species of Archizygoptera. Furthermore it became evident that the holotype of *Italophlebia gervasuttii* needed a thorough redescription, since it was only very briefly described and incompletely figured by Whalley (1986). The attribution of *Italophlebia gervasuttii* to Zygoptera - Hemiphlebioidea by Whalley (1986) was exclusively based on superficial similarities and obvious symplesiomorphies and thus rather doubtful, so that a new assessment of the phylogenetic position of this interesting species was necessary, based on the methods of Phylogenetic Systematics. In the course of this task, the classification of Triassic odonates turned out to be a real mess of paraphyletic, polyphyletic and incorrectly placed taxa, so that a complete revision of the phylogenetic relationships of all genera of Triassic odonates became an inevitable prerequisite for a correct phylogenetic attribution of *Italophlebia*.
In the following study I used the wing venation nomenclature of Riek (1976) and Riek & Kukalová-Peck (1984), amended by Nel *et al.* (1993) and Bechly (1996). I applied the new phylogenetic classification of Odonatoptera proposed by Bechly (1996), and amended by Bechly (1997). Very detailed informations concerning this new classification of Odonata (including the used terminology of odonate wing venation)

are available on the World Wide Web under the following Internet-address (URL): *http://members.aol.com/odonatadat/phylogeny/bechly.htm*. For the systematic analysis and classification I strictly followed the principles of consequent Phylogenetic Systematics (*sensu* Hennig 1966, 1981), rather than socalled „numerical cladistics" (for reasons see Wägele 1994, Boricki 1996, and Bechly 1997). All recognized monophyla have been named, since the sequencing of stem-group representatives should be rejected because of the logical and practical reasons described by Willmann (1989). Redundant taxa and the assignment of formal categorial ranks has been omitted whenever possible without violation of the International Rules of Zoological Nomenclature, because they are absolutely arbitrary and more or less superfluous (Willmann 1989). For all „higher" taxa phylogenetic definitions are provided according to socalled „phylogenetic taxonomy" after De Queiroz & Gauthier (1990, 1992). The preference of „phylogenetic taxonomy" is not dependent on the view of taxa as real entities (individuals), since it is dealing with the definition of names rather than groups, so that this approach is equally useful and even more preferable if taxa are understood as concepts (natural kinds *sensu* Mahner & Bunge 1997).

GEOLOGY. The outcrop of Ponte Giurino village (about 15 km north of Bergamo town, Imagna Valley, Lombardy Basin, Bergamasc Prealps, Northern Italy) represents thick argillaceous basinal successions that accumulated at the bottom of depressions adjacent to intra-basinal palaeo-highs. This socalled Lower Argilliti di Riva di Solto Formation (AdS1) includes dark shales intercalated by compact, dark grey limestones and marly limestones, with a maximum total thickness of about 1000 m at the type locality (Garassino & Teruzzi 1993).
The AdS1 has been dated as of Upper Triassic origin, either Upper Norian or Rhaetian (Garassino & Teruzzi 1993).
The fossiliferous rock is a dark bituminous shale, easy to crumble because of rapid dehydration after extraction. Therefore the fossils have to be carefully dried, enrolled in paper under heavy weights (Garassino & Teruzzi 1993). The invertebrate fossils are compressed and flattened, so that the insect wings have not preserved the original corrugation of high and low veins.
The thanatocenosis of this locality includes shark teeth, actinopterygid fishes (mainly pholidophorids), a few terrestrial „reptiles" and the oldest known pterosaur (*Eudimorphodon*), echinoderm remains, insects, crustaceans (mainly thylacocephalans and decapods, and a few isopods), an aphroditid and an eunicid polychaete, few archaeogastropods and some lamellibranchiats (the latter two groups probably allochthonous) (Garassino & Teruzzi 1993; Renesto & Paganoni 1995; Wild 1995). Except the dragonfly specimens described below, and the beetle *Holcoptera schlotheimi* described by Whalley (1986), meanwhile numerous other fossil insects of different orders have been found but are not yet described (all deposited in the collection of the Museo Civico di Scienze Naturali «Enrico Caffi», Bergamo, Italy).
The AdS1 sea floor apparently had wholesale dominant anoxic conditions, with partly oxygenic phases, while the peripheral parts of the basin and the upper water column must have had oxygen enough to sustain a thriving benthonic and nectonic community (Jadoul *et al.* 1992). The insects as well as the terrestrial „reptiles" and a terrestrial

palynofacies indicate the relative proximity of emergent land (Zambelli 1986; Paganoni & Renesto 1995; Paganoni & Cirilli 1995).

SYSTEMATIC PALEONTOLOGY.

Genus *Italophlebia* Whalley 1986
(in Isophlebioptera - Parazygoptera - Triassolestidae - Triassothemistini pos. nov.)
Type-species: *Italophlebia gervasuttii* Whalley 1986.
Other species: *Italophlebia paganoniae* spec. nov.
New diagnosis: Body length about 50 mm; compound eyes separated but head not transversely elongated; pterothorax strong and abdomen distally somewhat expanded; anisopteroid anal appendages with two cerci and an epiproctal process; fore wing span about 69 mm; both wings distinctly petiolated and falcate; two primary and two secondary antenodal crossveins; the basal secondary antenodal crossvein is strictly aligned and enforced like a primary antenodal crossvein, and distinctly slanted towards the nodus; the most distal of the few antesubnodal crossveins is distinctly slanted towards the nodus; the subnodus is more or less transverse; about twelve postnodal crossveins between nodus and pterostigma (maybe less in *Italophlebia paganoniae* spec. nov.); pterostigma unbraced with about four crossveins beneath it; the arculus is close to Ax1; the bases of RP and MA are distinctly separated at the arculus; several antefurcal crossveins are present between RP and MA basal of the midfork; the origin of RP3/4 and IR2 is basal of the subnodus; the origin of RP2 is about three cells distal of the subnodus; RP1 and RP2 are distally strongly converging; the area between RP1 and RP2 is the only wing area between to longitudinal veins with more than one row of cells; IR1 is at least basally zigzagged; there are several pektinate posterior „branches" of the distal parts of RP3/4 and MP; there is no lestine oblique vein „O" between RP2 and IR2; the area between RP2 and IR2 is basally very narrow but distally widened; the area between IR2 and RP3/4 is basally narrow, then widened, and distally again constricted; MA is distally distinctly zigzagged; the distal discoidal vein MAb is perpendicular, aligned with the arculus in the fore wing, but distal of the arculus in the hind wing; the discoidal cell is basally open in the fore wing and basally closed in the hind wing; basal cell, subbasal cell, discoidal cell, and subdiscoidal cell are free of crossveins; MA and MP are closely parallel; the postdiscoidal area is narrow with only one row of cells till the wing margin; CuA is distally zigzagged; there is a row of transversely elongated cells between MP and CuA, between MP and the hind margin, and between CuA and the hind margin; the CuP-crossing is close to the level of Ax1 in the fore wing, but much more basal in the hind wing; in the fore wing [AA & CuP] is free and ends on CuAb (subdiscoidal cell posteriorly closed); in the hind wing [AA & CuP] is shortly fused to [MP& CuA] near the arculus, and the distal free part is perpendicular, aligned with the arculus, and ending on the hind margin (subdiscoidal cell posteriorly open); male hind wings with a distinct anal angle.

Italophlebia gervasuttii Whalley 1986
figures 1-6

- 1986 *Italophlebia gervasuttii*, Whalley, pp. 51-60, figs 1-8. (in Zygoptera - Hemiphlebioidea - Italophlebiidae fam. nov.).
- 1994 *Italophlebia gervasuttii* Whalley; Bridges, pp. III.24 and VII.97. (in Zygoptera - Hemiphlebioidea - Italophlebiidae fam. nov.).
- 1996 *Italophlebia gervasuttii* Whalley; Ansorge, p. 19, (in „Anisozygoptera" - Oreopteridae).
- 1996 *Italophlebia gervasuttii* Whalley; Bechly, p. 361, (in Triassoneuridae sensu nov., of which Italophlebiidae and Triassothemistidae were regarded as junior subjective synonyms).

Holotype: Specimen no. [3460a,b], Museo Civico di Scienze Naturali «Enrico Caffi», Bergamo, Italy.

Paratypes: Whalley (1986) designated specimen no. [6678] in the Museo Civico di Scienze Naturali «Enrico Caffi» (Bergamo / Italy) as paratype of *Italophlebia gervasuttii*; however this specimen is representing a new genus and species of Archizygoptera described below.

Other specimens: Specimens no. [5115] and [6677a,b] mentioned by Whalley (1986), and a new female hind wing, no. [9500], all in the Museo Civico di Scienze Naturali «Enrico Caffi», Bergamo, Italy. During my visit at Bergamo in September 1996 unfortunately I could not find specimen [5115], which shall represent a relatively complete but very poorly preserved specimen of *Italophlebia gervasuttii* according to Whalley (1986).

Horizon and locality: Upper Triassic, Upper Norian or Rhaetian, bituminous shales of the lower Argilliti di Riva di Solto Formation (AdS1), Ponte Giurino village (about 15 km north of Bergamo town), Imagna Valley, Lombardy Basin, Bergamasc Prealps, Northern Italy.

New diagnosis: Differing from *Italophlebia paganoniae* spec. nov. in the following characters: Fore wing distinctly less slender, but of similar length; the postnodal crossveins and the postsubnodal crossveins between RA and RP are more densely spaced; about twelve poststigmal crossveins between the costal margin and RA, instead of probably only six or seven; area between RP1 and RP2 distinctly less narrow, with two rows of regular transversely elongate cells in the distal half of the interspace; IR1 present, but basally zigzagged; several pektinate posterior „branches" of RP2; IR2 originating more basally, distinctly closer to RP3/4 than to RP2; MP reaching till the level of the pterostigma.

Redescription:

Holotype specimen no. [3460a,b] labelled [Museo Civico di Scienze Naturali «Enrico Caffi» - Bergamo / E S. 758 Pos. Olotipo / Insecta. Odonata. / Italophlebia gervasuttii, Whalley 1986. / Età Triassico superiore / Loc. P. te Giurino. / Paleontologia Bergamasca] (figures 1-5)

Part and counterpart of a well preserved complete male dragonfly, with head, thorax, abdomen and all four wing in outspread position; only the legs are not preserved. The wings show nearly all details of the venation, with exception of the distal part of the left fore wing. The wings are flattened and have not preserved the original corrugation.

Fig. 1 - Photo of *Italophlebia gervasuttii* (holotype no. 3460a; part).
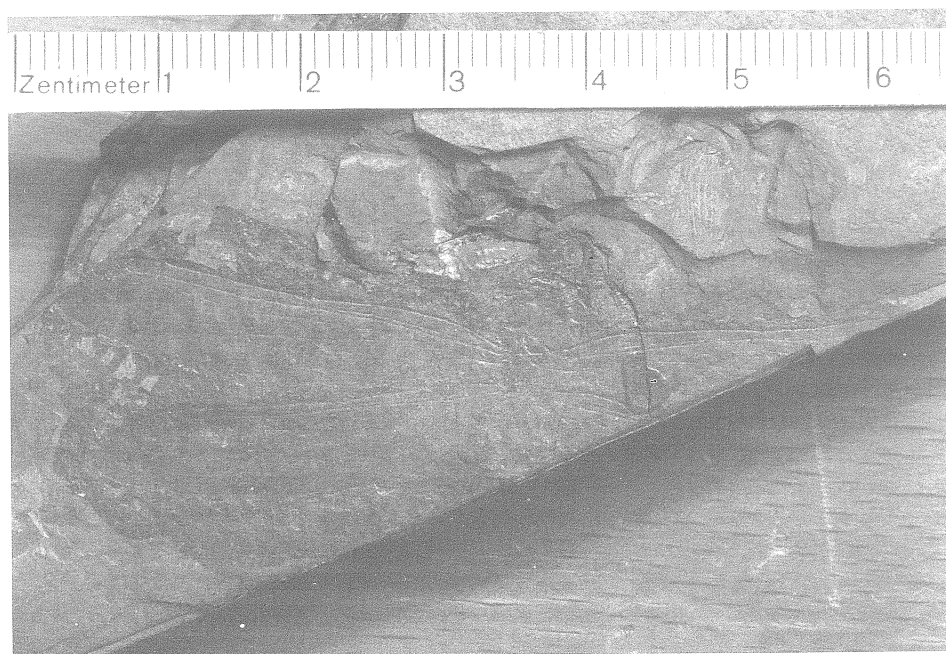
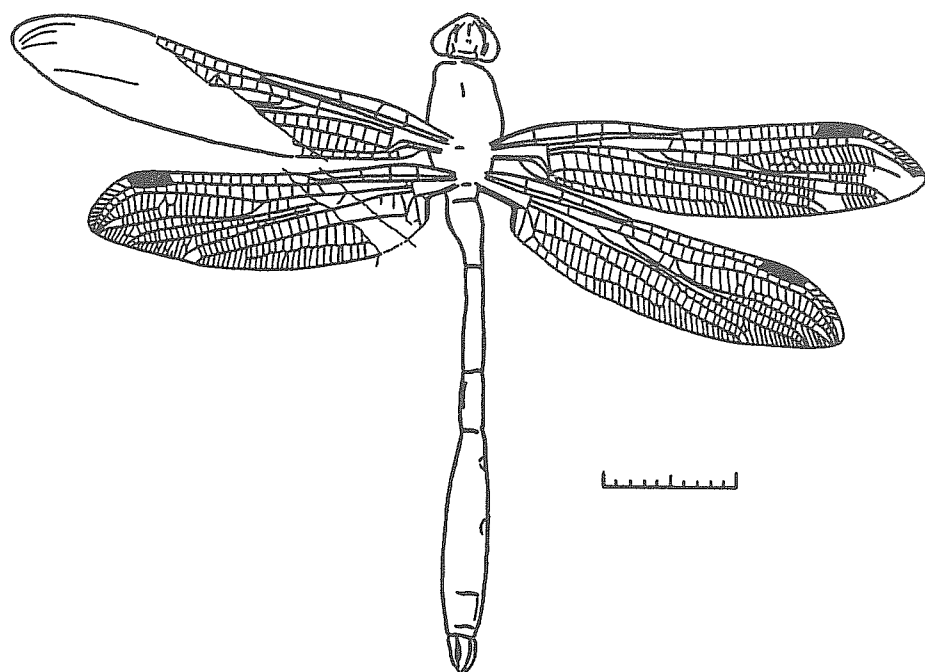Fig. 2 - Photo of *Italophlebia gervasuttii* (holotype no. 3460b; counterpart).

Fig. 3 - Reconstruction of *Italophlebia gervasuttii* (holotype no. 3460a,b; combined from part and counterpart; scale 10 mm).
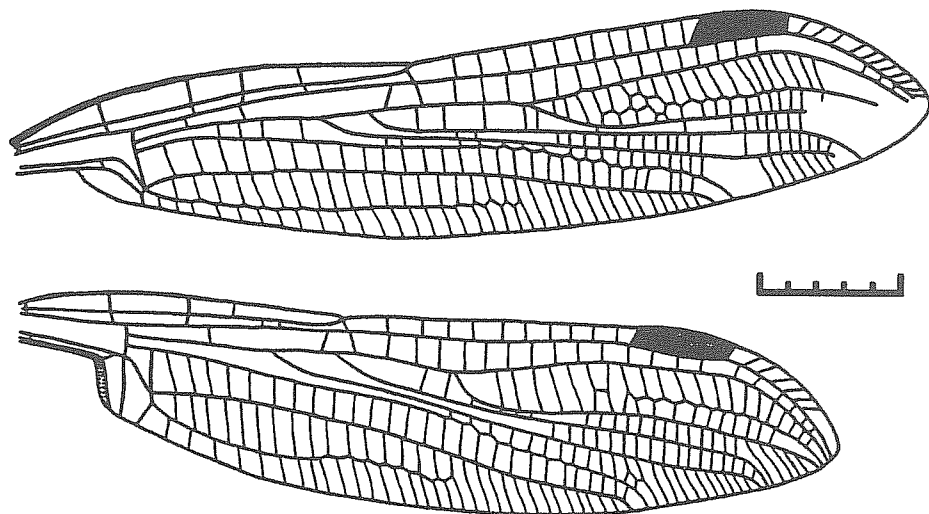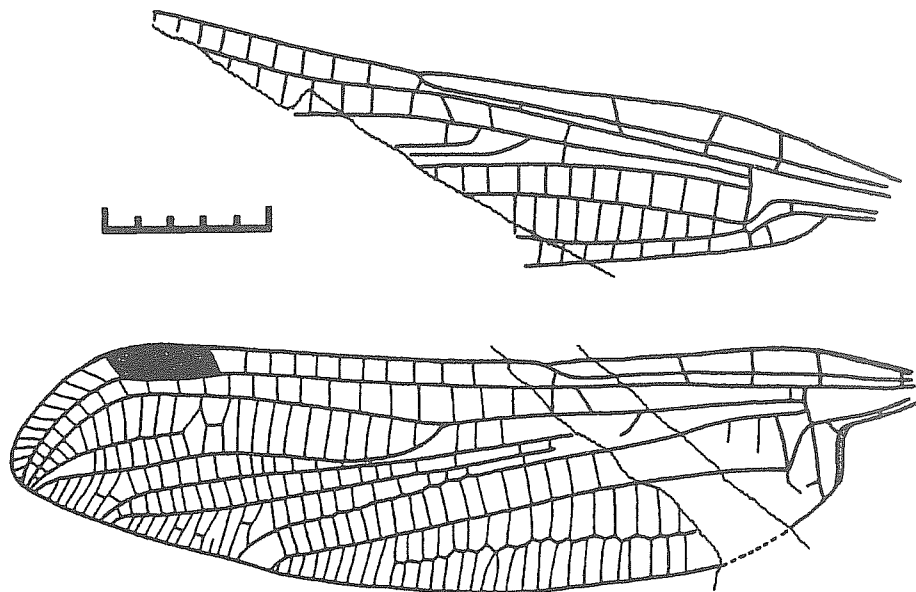

Fig. 4 - Drawing of right wing pair of *Italophlebia gervasuttii* (holotype no. 3460a,b; combined from part end counterpart; scale 5 mm).

There is no preserved colour pattern of the wings, which probably have been hyaline except the pterostigma.

Figure 5 - Drawing of left wing pair of *Italophlebia gervasuttii* (holotype no. 3460a,b; combined from part end counterpart; scale 5 mm).

Please note: In the following description at statement like „14 / 16 mm" means „14 mm in the right wing" and „16 mm in the left wing". If there is only one value stated, this value is equal in both wings or the character is only preserved in one of the two wings. Fore wings: Length, 32.1 mm; width, 6.7 mm (midway between nodus and pterostigma); the two primary antenodal crossveins Ax1 and Ax2 are aligned and stronger than the secondaries; Ax1 is 3.1 / 3.6 mm distal of the basal brace Ax0, and Ax2 is about 3.1 / 2.3 mm distal of Ax1; there are no secondary antenodals between Ax1 and Ax2; there are two secondary antenodals distal of Ax2, between costal margin and ScP and between ScP and RA, which are more or less aligned, the basal one even being enforced (looking like a primary antenodal crossvein) and slanted towards the nodus; the arculus is situated close to Ax1 (0.8 mm distal of it); distance from wing base to nodus 14.3 / 15.1 mm; the nodal veinlet is somewhat oblique and very close to the nodus (point of fusion of ScP with the costal margin); the subnodal veinlet is aligned with the nodal veinlet and is less oblique (right fore wing) or even transverse (left fore wing); there are three antesubnodal crossveins preserved, of which the most distal is distinctly slanted towards the nodus; distance from nodus to pterostigma, 9.9 mm; there are twelve postnodal crossveins between nodus and pterostigma in the right fore wing, of which only nine are preserved in the left one; there are eleven poststigmal crossveins preserved between the costal margin and RA, but there were probably one or two more; the postsubnodal crossveins are not aligned with the corresponding

postnodal crossveins; the pterostigma is 3.3 mm long and max. 1.0 mm broad; the pterostigma is unbraced and there are four crossveins preserved beneath the pterostigma, but there might have been five of them (in the right fore wing); ScP is not smoothly converging to the costal margin but distinctly curved near the nodal veinlet; RP1 and RP2 probably were distally strongly converging, but the referring area is not completely preserved; between RP1 and RP2 there are one to three rows of cells basal of the pterostigma, two rows beneath the pterostigma, and two rows distal of the pterostigma; IR1 is distally straight and basally zigzagged, and reaches till basal of the pterostigma; RP2 originates 5.9 mm basal of the pterostigma; the distal part of RP2 is not preserved in both fore wings, therefore it is unknown if there were pektinate posterior branches as in the hind wings; the area between RP2 and IR2 is basally very narrow but widens distally; there is only one row of cells between RP1/2 or RP2 and IR2; there is no lestine oblique vein „O" visible between RP2 and IR2; IR2 is straight and originates on RP1/2 four cells and 5.7 mm basal of RP2 (1.9 / 2.2 mm basal of the subnodus); the area between IR2 and RP3/4 is basally narrow, then widened, and towards the wing margin again constricted; there are no crossveins between the origins of IR2 and RP3/4; RP3/4 originates 7.3 mm basal of RP2 (3.6 mm / 3.8 mm basal of the subnodus) and is straight till the wing margin; there are several (seven preserved) pektinate posterior „branches" of RP3/4 between the latter and MA; there are four / one antefurcal crossveins preserved between RP3/4 and MA basal of the midfork; MA is distinctly zigzagged in the distal half; MP is more or less closely parallel to MA, but near the wing margin the two veins are converging; there is only one row of cells in the narrow postdiscoidal area till the wing margin; MP reaches till the level of the pterostigma and there are fifteen pektinate posterior „branches" of MP between the latter and CuA; CuA is strongly zigzagged and distally vanishing; there is a characteristical row of transversely elongate cells between MP and CuA, between MP and the hind margin, and between CuA and the hind margin; there is small branch CuAb beneath the tip of the discoidal cell; [AA & CuP] is not fused to [MP & CuA] and ends on CuAb; the subdiscoidal cell is normal (posteriorly closed); the discoidal cell is basally open and free of crossveins; the distal discoidal vein MAb is 1.3 / 1.0 mm long, nearly perpendicular and rather straight; MAb is aligned with the arculus; the basal cell and subbasal cell are free of crossveins; the CuP-crossing (= anal-crossing auct.) is situated slightly basal of the level of Ax1; the anal margin is rounded; the anal area basal of CuAb seems to be free in the right fore wing, but is traversed by one crossvein in the left one; the wing is distinctly petiolated (length of petiole, 2.0 mm; width at end of petiole, 2.2 / 1.9 mm).

Hind wings: Length, 29.1 / 27.4 mm; width, 6.7 / 6.9 mm (midway between nodus and pterostigma); the two primary antenodal crossveins Ax1 and Ax2 are aligned and stronger than the secondaries; Ax1 is 2.9 / 2.4 mm distal of the basal brace Ax0, and Ax2 is about 2.7 / 2.1 mm distal of Ax1; there are no secondary antenodals between Ax1 and Ax2; in the right hind wing there is one basal secondary antenodal distal of Ax2 visible between costal margin and ScP, and two more distal ones between ScP and RA, in the left hind wing there is one antenodal visible distal of Ax2 which is looking like a primary antenodal and is distinctly slanted towards the nodus; the arculus is situated close to Ax1 (0.4 mm distal of it); distance from wing base to nodus, 11.4 /

11.3 mm; the nodal veinlet is somewhat oblique and very close to the nodus (point of fusion of ScP with the costal margin); the subnodal veinlet is aligned with the nodal veinlet and somewhat less oblique in the right hind wing, and transverse in the left one; there are two / one antesubnodal crossveins preserved, of which the most distal is distinctly slanted towards the nodus; distance from nodus to pterostigma, 10.1 / 9.9 mm; there are ten / eleven postnodal crossveins between nodus and pterostigma; there are eleven poststigmal crossveins between the costal margin and RA in the left hind wing, while only six are preserved in the right one; the postsubnodal crossveins are not aligned with the corresponding postnodal crossveins; the pterostigma is 3.4 / 2.9 mm long and max. 1.0 / 1.1 mm broad; the pterostigma is unbraced and there are three crossveins beneath the pterostigma; ScP is not smoothly converging to the costal margin but distinctly curved near the nodal veinlet; RP1 and RP2 are distally strongly converging, with only two small cells between them at the wing margin; between RP1 and RP2 there is one row of cells basal of the pterostigma, two rows beneath the pterostigma, and two rows distal of the pterostigma; IR1 is distally straight and basally zigzagged, and reaches till the level of the middle of the pterostigma; RP2 originates 6.1 / 6.7 mm basal of the pterostigma; there are five / six pektinate posterior „branches" of RP2 between the latter and IR2; the area between RP2 and IR2 is basally very narrow but widens distally; there is only one row of cells between RP1/2 or RP2 and IR2; there is no lestine oblique vein „O" visible between RP2 and IR2; IR2 is straight and originates on RP1/2 4.2 mm basal of RP2 (0.7 mm basal of the subnodus); the area between IR2 and RP3/4 is basally narrow, then widened, and towards the wing margin again constricted; there are no crossveins between the origins of IR2 and RP3/4; RP3/4 originates 6.5 / 6.0 mm basal of RP2 (2.9 / 2.7 mm basal of the subnodus) and is straight till the wing margin; there are eleven pektinate posterior „branches" of RP3/4 between the latter and MA; there are no preserved antefurcal crossvein between RP3/4 and MA basal of the midfork; MA is distinctly zigzagged in the distal half; MP is more or less closely parallel to MA, but near the wing margin the two veins are converging (less so in the left hind wing); there is only one row of cells in the narrow postdiscoidal area till the wing margin; MP reaches till the level of the pterostigma in the right hind wing, but ends somewhat basal of it in the left hind wing; there are fourteen / ten pektinate posterior „branches" of MP between the latter and CuA; CuA is strongly zigzagged and distally vanishing; there is a characteristical row of transversely elongate cells between MP and CuA, between MP and the hind margin, and between CuA and the hind margin; there is a relatively short and straight branch CuAb beneath the tip of the discoidal cell, with a distinct angle between it and the „gaff"-portion of CuA; [AA & CuP] is shortly fused to [MP & CuA] basal of the arculus (length of fusion 0.4 / 0.5 mm); the basal free part of [AA & CuP] is very short, oblique, and slightly curved, and looks like a CuP-crossing; the distal free part of [AA & CuP] is long and straight, and perpendicularly running to the hind margin beneath the arculus (aligned with it), and thus is not reaching CuA; consequently the subdiscoidal cell is posteriorly open; the discoidal cell is 0.9 / 1.0 mm long (anterior side), free of crossveins, and basally closed by the posterior part of the arculus; the distal discoidal vein MAb is 1.4 / 1.6 long, nearly perpendicular and rather straight (weakly concave in the left hind wing); vein MAb is shifted distal of the arculus; the

basal cell and subbasal cell are free of crossveins; the CuP-crossing is in a very basal position (3.3 / 2.1 mm basal of the arculus); there is a distinct anal angle on the level of the perpendicular branch of [AA & CuP], thus it is a male specimen; the wing is distinctly petiolated (length of petiole, 2.9 / 2.4 mm; width at end of petiole, 2.3 / 2.2 mm); there is a narrow membranule along the anal margin of the wing (width about 0.3 / 0.1 mm).

Body: The head is only poorly preserved in the part of the holotype, but in the counterpart there are some details visible. It is obviously preserved in ventral aspect. The compound eyes seem to be separated, but the head is not transversely expanded as in Zygoptera. The max. width of the head is, 5.1 mm. The pterothorax is not very well preserved but it was rather strong (length, 9.2 mm; max. width, 5.7 mm). None of the legs is preserved. The abdomen is 33.8 mm long (excl. anal appendages). It is basally expanded at the position of the secondary genital apparatus (segment II; max. width, 2.7 mm) and distally somewhat expanded too (segment VI-X; max. width, 3.2 mm), while the median part (segment III-V) is rather slender (width, 1.6 mm). The anal appendages are preserved too and include two cerci (length, 2.4 mm; width, 0.5 mm), and a conical epiproctal process (length, 2.7 mm). There are no traces of lateral auricles on segment II (*contra* Whalley 1986).

Whalley (1986) mentioned that the holotype of *Italophlebia gervasuttii* represents the oldest record of an odonate secondary male genital apparatus. This statement cannot longer be regarded as correct: A secondary genital apparatus is also preserved in some specimens of Permian Protozygoptera and Protanisoptera in the collections of the Paleontological Institute in Moscow (recently confirmed by Nel pers. comm.). Since two fossil wings of Protozygoptera are meanwhile also known from the Upper Carboniferous (unpubl. pers. observ. on a specimen from Carrizo Arroyo / New Mexico in coll. Kukalová-Peck, and Nel pers. comm.), the secondary genital apparatus must have been present in this time too. Consequently this unique and complex structure has a surprisingly early origin in the evolution of pterygote insects (Bechly & Lindeboom in prep.).

New specimen no. [9500] labelled [Museo Civico di Scienze Naturali «Enrico Caffi» - Bergamo / S. 1562 Liv. 36 Z Ott. 93 / Libellula ala / Paleontologia Bergamasca] (figure 6)
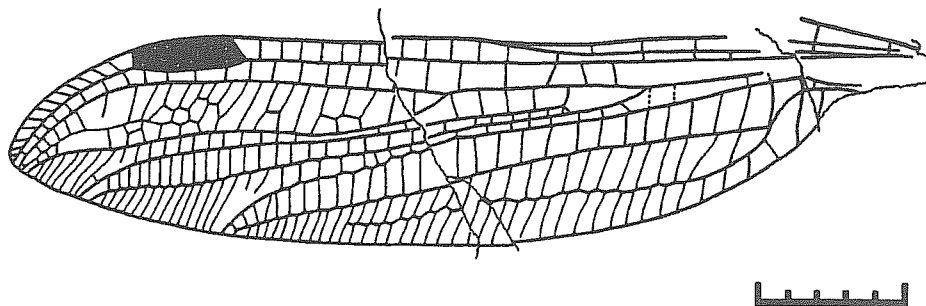

Fig. 6 - Drawing of female hind wing of *Italophlebia gervasuttii* (specimen no. 9500; scale 5 mm).

A complete and well preserved isolated left hind wing of a female specimen. Length of the wing, 30.4 mm (corrected value); width, 6.9 mm (midway between nodus and pterostigma); the basal brace Ax0 is preserved; the two primary antenodal crossveins Ax1 and Ax2 are aligned and stronger than the secondaries; Ax1 is 2.6 mm distal of Ax0, and Ax2 is about 2.4 mm distal of Ax1; there are no secondary antenodals between Ax1 and Ax2; there are two secondary antenodals distal of Ax2, between costal margin and ScP and between ScP and RA, that are imperfectly aligned; the arculus is situated close to Ax1; distance between wing base and nodus, 13.4 mm (corrected value); the nodal veinlet is transverse and 1.7 mm basal of the nodus (point of fusion of ScP with the costal margin); the subnodal veinlet is aligned with the nodal veinlet and somewhat oblique; there are two antesubnodal crossveins preserved close to the subnodus, of which the most distal is slightly slanted towards the nodus; distance between nodus and pterostigma, 9.0 mm; there are twelve postnodal crossveins between nodus and pterostigma, of which the most basal is directly at the nodus; there are twelve poststigmal crossveins between the costal margin and RA; the postsubnodal crossveins are not aligned with the corresponding postnodal crossveins; the pterostigma is 3.7 mm long and max. 1.1 mm broad; the pterostigma is unbraced and there are four crossveins beneath the pterostigma; ScP is smoothly converging to the costal margin; RP1 and RP2 are distally strongly converging, with only two small cells between them at the wing margin; between RP1 and RP2 there are one or two rows of cells basal of the pterostigma, two or three rows beneath the pterostigma, and two rows distal of the pterostigma; IR1 is short and zigzagged (ending beneath the middle of the pterostigma); RP2 originates 6.7 mm basal of the pterostigma; there are seven pektinate posterior „branches" of RP2 between the latter and IR2; the area between RP2 and IR2 is basally very narrow but widens distally; there is only one row of cells between RP1/2 or RP2 and IR2; there is no lestine oblique vein „O" visible between RP2 and IR2; IR2 is straight and originates on RP1/2 four cells and 4.2 mm basal of RP2 (0.7 mm basal of the subnodus); the area between IR2 and RP3/4 is basally narrow, then distinctly widened, and towards the wing margin again constricted; there are no crossveins between the origins of IR2 and RP3/4; RP3/4 originates 6.8 mm basal of RP2 and is distally zigzagged; there are fourteen pektinate posterior „branches" of RP3/4 between the latter and MA; there seem to be several (four faintly preserved) antefurcal crossveins between RP3/4 and MA basal of the midfork; MA is distinctly zigzagged in the distal half; MP is parallel to MA, but near the wing margin the two veins are strongly converging; there is only one row of cells in the postdiscoidal area till the wing margin; MP reaches till the level of the pterostigma and there are eleven pektinate posterior „branches" of MP between the latter and CuA; CuA is strongly zigzagged and distally vanishing; there is a characteristical row of transversely elongate cells between MP and CuA, between MP and the hind margin, and between CuA and the hind margin; there is small branch CuAb beneath the tip of the discoidal cell, with a distinct angle between it and the „gaff"-portion of CuA; [AA & CuP] is fused to [MP & CuA] basal of the arculus; the distal free part of [AA & CuP] is perpendicularly running to the hind margin beneath the arculus, and thus is not reaching CuA; consequently the subdiscoidal cell is posteriorly open; the discoidal cell is 1.0 mm long (anterior side), free of crossveins, and basally closed by the posterior

part of the arculus; the distal discoidal vein MAb is 1.5 long, nearly perpendicular and concavely curved; vein MAb is shifted distal of the arculus; the basal cell is free of crossveins; the anal margin is rounded, there is no anal angle, thus it is almost certainly a female specimen; the wing probably was distinctly petiolated, but unfortunately the posterior part of the wing base is not preserved; the apparent wing base of this fore wing, which is situated basal of a crack-line along the level of the arculus, is indeed not the wing base of the same wing but of the second fore wing, concealed underneath, which is clearly evident from the simple fact that the basal discoidal vein and the perpendicular branch of [AA & CuP] are present basal as well as distal of the crack-line.

Discussion: Behalf the absence of an anal angle, which can easily be attributed to sexual dimorphism, this wing has several noteworthy differences to the hind wings of the holotype: ScP smoothly converging to the costal margin instead o being distinctly curved; nodal veinlet much basal of the nodus instead of being very close to it; nodal veinlet transverse instead of oblique; subnodus oblique instead of transverse; most basal postnodal and postsubnodal crossvein situated at the nodus instead of distinctly distal of it; most basal antesubnodal crossvein only indistinctly slanted towards the nodus; absence of the characteristical pattern of transversely elongate cells in two rows between RP1 and RP2; the distal area between IR2 and RP3/4 is more strongly widened before the final constriction; RP3/4 is distally zigzagged; the most basal secondary antenodal crossvein is not strictly aligned and enforced like a primary antenodal crossvein, and not slanted towards the nodus.

It is very well possible that this wing belongs to a different species of *Italophlebia*, but almost certainly not to *Italophlebia paganoniae* spec. nov. (compare diagnoses). Until further material becomes available I preliminarily prefer to regard this wing as a (maybe somewhat aberrant) female hind wing of *Italophlebia gervasuttii*. This view is partly supported by the surprising differences between the right and left wing pair in the holotype, although these rather refer to relative positions and lengths, than to the differences just mentioned. However there seems to have been a relatively large degree of variability in the wing venation of *Italophlebia*.

Specimen no. [6677a,b] labelled [Museo Civico di Scienze Naturali «Enrico Caffi» - Bergamo / Es. 741 / Italophlebia gervasuttii / Età Triassico sup. Norico / Loc. P. te Giurino. / Paleontologia Bergamasca]
Part and counterpart of a relatively poorly preserved isolated fore wing.
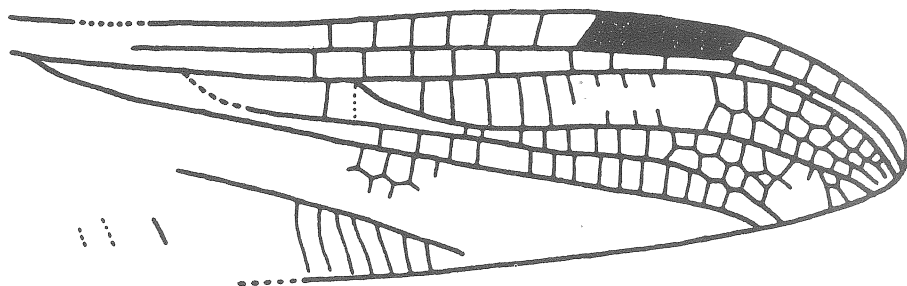

Italophlebia paganoniae spec. nov.
figures 7-8

Holotype: Specimen no. [6679], Museo Civico di Scienze Naturali «Enrico Caffi», Bergamo, Italy. This specimen was erroneously regarded as another specimen of *Italophlebia gervasuttii* by Whalley (1986). No further specimens known yet.

Horizon and locality: Upper Triassic, Upper Norian or Rhaetian, bituminous shales of the lower Argilliti di Riva di Solto Formation (AdS1), Ponte Giurino village (about 15 km north of Bergamo town), Imagna Valley, Lombardy Basin, Bergamasc Prealps, Northern Italy.
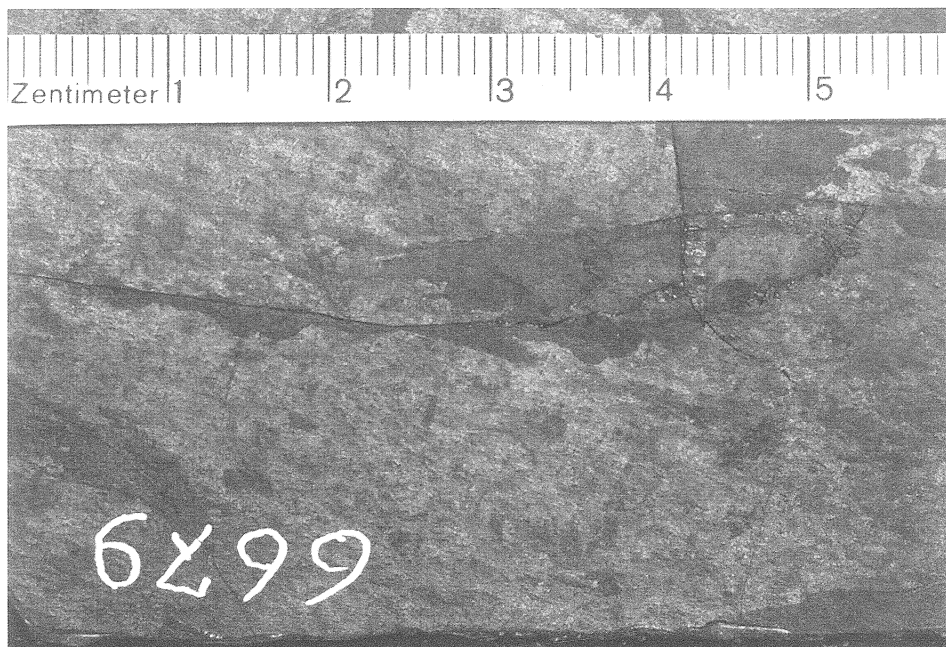
Fig. 7 - Photo of *Italophlebia paganoniae* spec. nov. (holotype no. 6679).

Fig. 8 - Drawing of *Italophlebia paganoniae* spec. nov. (holotype no. 6679; scale 5 mm).

Etymology: Named in honour of Dr. Anna Paganoni (Bergamo), director of field research in Ponte Giurino.

Diagnosis: Differing from *Italophlebia gervasuttii* in the following characters: Fore wing distinctly more slender, but of similar length; the postnodal crossveins and the postsubnodal crossveins between RA and RP are more widely spaced; probably only about six or seven poststigmal crossveins between the costal margin and RA, instead of about twelve; area between RP1 and RP2 distinctly more narrow, without the two rows of regular transversely elongate cells; IR1 completely reduced; no pectinate posterior „branches" of RP2; IR2 originating more distally, about halfway between RP3/4 and RP2; MP not reaching till the level of the pterostigma.

Description:

Holotype specimen no. [6679] labelled [Museo Civico di Scienze Naturali «Enrico Caffi» - Bergamo / E S. 741 / Insecta. Odonata. / Italophlebia gervasuttii, Whalley 1986. / Età Triassico sup. Norico / Loc. P. te Giurino. / Paleontologia Bergamasca]

An isolated fore wing of which only the apical third is rather well preserved. Length of the complete wing, 31.8 mm; width, 5.9 mm (midway between nodus and pterostigma); the postnodal crossveins are not aligned with the corresponding crossveins between RA and RP; the pterostigma is 3.6 mm long and max. 0.9 mm wide; it is unbraced and there are only two or maybe three crossveins beneath it; there are only three poststigmal crossveins preserved between the costal margin and RA, but there were probably six or seven of them; the area of the nodus is not preserved; IR1 is completely reduced; RP2 originates 5.2 mm basal of the pterostigma, and distally converges with RP1 (only separated from the latter by three cells at the wing margin); there is only one row of cells between RP1 and RP2 basal of the pterostigma, and more distal there is an irregular meshwork of cross-venation (max. three rows of cells between RP1 and RP2); IR2 originates about 4.0 mm basal of RP2 and is distally slightly zigzagged; there are no posterior „branches" on the distal part of RP2; between the distal parts of RP2 and IR2 there is just an open meshwork of cross-venation; the area between IR2 and RP3/4 is basally and distally narrow, but slightly widened in the median part; RP3/4 originates 7.6 mm basal of RP2 and runs close to IR2, with only one row of cells between these veins till the wing margin; only a very short part of the zigzagged vein MA is preserved; MP is distally diverging from RP3/4, with about 6.7 mm between these veins along the wing margin, MP does not reach till the level of the pterostigma; there are numerous pektinate posterior „branches" of MP; CuA and the basal part of the wing, including the discoidal area, is not preserved.

Discussion: The mentioned differences between this wing and the known specimens of *Italophlebia gervasuttii* certainly justify the attribution to a new species. The attribution of this new species to the genus *Italophlebia* is based on the following characters: Lestine oblique vein „O" is suppressed (derived trend in Parazygoptera); RP2 originating distinctly distal of the subnodus (synapomorphy with Parazygoptera); area between IR2 and RP3/4 basally very narrow, then expanded, and distally again narrowed (synapomorphy with Triassothemistini); area between RP2 and IR2 basally very narrow (synapomorphy with Triassothemistini); RP1 and RP2 distally converging (synapomorphy with *Italophlebia*); MA distally zigzagged (synapomorphy with *Italophlebia*); IR1 short and zigzagged (synapomorphy with *Italophlebia*).

Phylogenetic position of *Italophlebia* and its taxonomical implications:
Whalley (1986) described *Italophlebia* in a monotypic family Italophlebiidae within Zygoptera - Hemiphlebioidea (followed by Bridges 1994). This position would be most surprising since until recently Hemiphlebioidea were only known from a single Recent species *Hemiphlebia mirabilis* (Hemiphlebiidae) in Southern Australia, while the first genuine fossil Hemiphlebiidae are described from the Lower Cretaceous of Brazil by Bechly *et al.* (in print). Whalley's conclusion was based on the following two similarities: Discoidal cell basally open in fore wings and basally closed in hind wings; and postnodal crossveins non-aligned with the postsubnodal crossveins. However these arguments are ill founded since both mentioned similarities clearly are symplesiomorphies (see Bechly 1996). Indeed *Italophlebia* shares neither any convincing synapomorphies with Hemiphlebiidae nor with Zygoptera.
Ansorge (1996: 19) supposed that *Italophlebia* might be an Oreopteridae, but also mentioned that the figures in the original description are not sufficient for a definite attribution.
Bechly (1996) synonymised Italophlebiidae and Triassothemistidae with Triassoneuridae, which he regarded as Odonata *incertae sedis*. He also included *Triassolestodes* but not *Triassolestes*, and transferred „*Triassothemis*" *nipponensis* and „*Triassoneura*" *okafujii* to the Progonophlebiidae.
Italophlebia shares the following synapomorphies with Epiproctophora (= Epiophlebiidae & Anisoptera, including their stem-groups): Arculus shifted basally in a position between the two primary antenodals Ax1 and Ax2; distinct anal angle in male hind wings; costal margin not indented at node, since the costal margin basal of the nodus is in line with the costal margin distal of the nodus instead of being curved on it; secondary epiproctal projection as single inferior appendage in adult males; thorax and abdomen are relatively strong and stout.
Furthermore *Italophlebia* shares several synapomorphies with Euryoptera (Anisoptera and its stem-group, but excluding Epiophlebiidae): Distal discoidal vein MAb at least less oblique in the fore wing and transverse or even of reversed obliquity in the hind wing; cubito-anal field secondarily expanded in hind wings; secondary branching of the CuA into an antererior longitudinal branch CuAa and a posterior transverse branch CuAb; male hind wings with an anal triangle; adult males with completely suppressed paraprocts (zygopteroid paired appendices inferiores).
Therefore *Italophlebia* is here transferred from Zygoptera - Hemiphlebioidea to Euryoptera within Epiproctophora (Bechly 1996, 1997).
Within this monophyletic group *Italophlebia* is identified as member of the clade Isophlebioptera (Bechly 1996, 1997) by the following synapomorphies: In hind wings the subdiscoidal cell is distinctly widened, correlated with a unique course of the anal vein AA, which is strongly bent towards the posterior wing margin near the CuP-crossing; RP3/4 rather parallel to IR2, thus the space between RP3/4 and MA is distinctly expanded and traversed by several pektinate convex „secondary branches" of RP3/4; postdiscoidal space between MP and MA very narrow, with only one row of cells between them in the ground-plan; CuAa shortened and postero-distally indistinct (zigzagged), thus the distal space between MP and CuAa strongly expanded; distal of

Ax2 most or all antenodal crossveins between the costal margin and ScP are suppressed (convergent to Heterophlebioidea; reversed in Isophlebiidae).

Italophlebia obviously does not belong to the higher Isophlebioptera (Isophlebiida and Isophlebioidea *sensu* Bechly 1996, 1997) since they lack the derived elongated and recessed pterostigmata and the more strongly elongated „gaff" (base of CuA between discoidal cell and the first branching of CuA).

According to the present phylogenetic analysis *Italophlebia* belongs to a previously unrecognised clade within the isophlebioid „anisozygopteres" (viz. Isophlebioptera) that is also including the former taxa Oreopteridae, Asiopteridae, Cyclothemistidae, Progonophlebiidae, Mesophlebiidae, Triassolestidae (incl. *Triassolestodes asiaticus* Pritykina 1981), Triassoneuridae (except „*Triassoneura*" *primitiva* Pritykina 1981) and Triassothemistidae, as well as the genera *Proeuthemis* Nel & Jarzembowski 1996, *Sphenophlebia* Bode 1953, *Mesoepiophlebia* Nel & Henrotay in Nel *et al.* 1993 and *Ensphingophlebia* Bode 1953. This clade is here recognised for the first time and named as new taxon Parazygoptera. Since some of the mentioned families turned out to be paraphyletic or even polyphyletic, a new phylogenetic classification of all Parazygoptera is proposed below, including a list of the referring synapomorphies.

Since *Italophlebia* turns out to be a member of the „anisozygopteroid" grade, it has to be regarded as one of the oldest known stem-group representatives of Anisoptera (the Australian, South African and Japanese Triassic Parazygoptera are of Carnian age, thus somewhat older than *Italophlebia*; *Triassolestodes* is of Norian age like *Italophlebia*). Therefore the splitting events between Zygoptera and Epiproctophora (Epiophlebiidae & Anisoptera), as well as the splitting event between Epiophlebiidae and Anisoptera, and the branching of Isophlebioptera from the anisopterid stem-line, must be older than Upper Triassic („terminus post quem non" *sensu* Hennig).

<center>Genus Italomyrmeleon gen. nov.</center>
<center>(in Archizygoptera - Protomyrmeleontinae)</center>

Type-species: *Italomyrmeleon bergomensis* spec. nov.

Etymology: After Italy and the generic name „*Myrmeleon*".

Diagnosis: A typical but relatively large Protomyrmeleontinae with a wing length of more than 40 mm; the pterostigma is short and broad, with only one crossvein beneath it, and apparently braced; IR1 is long and straight; IR1, RP2, and IR2 are basally fused and originate with their common stem on RP3/4; RP2 is distally forked; RP3/4 and MA are parallel and curved towards the hind margin; there are about 17 postnodal crossveins between nodus and pterostigma.

<center>Italomyrmeleon bergomensis spec. nov.</center>
<center>figures 9-10</center>

Holotype: Specimen no. [6678], Museo Civico di Scienze Naturali «Enrico Caffi», Bergamo, Italy. This specimen was erroneously designated as paratype of *Italophlebia gervasuttii* by Whalley (1986). No further specimens known yet.
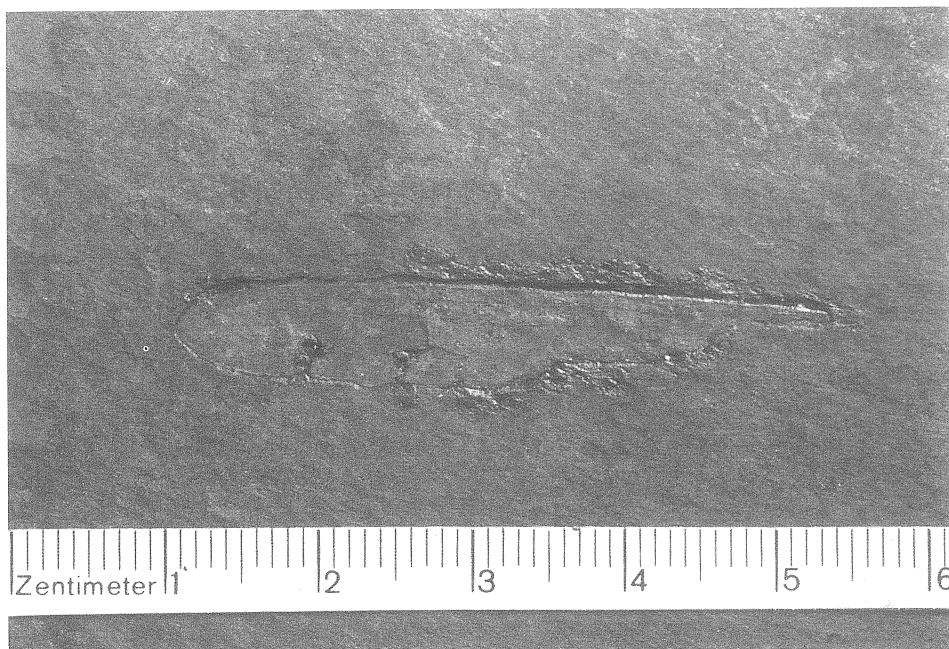
Fig. 9 - Photo of *Italomyrmeleon bergomensis* gen. et spec. nov. (holotype no. 6678).
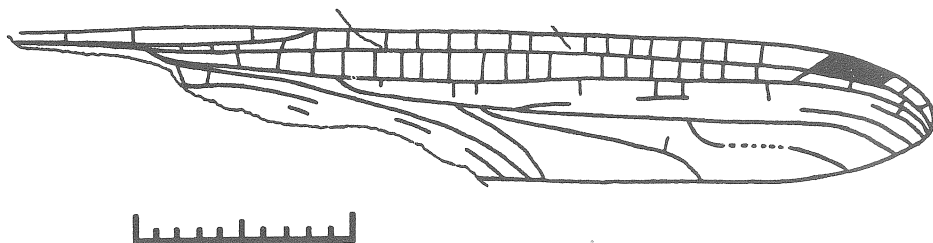

Fig. 10 - Drawing of *Italomyrmeleon bergomensis* gen. et spec. nov. (holotype no. 6678; scale 10 mm).

Horizon and locality: Upper Triassic, Upper Norian or Rhaetian, bituminous shales of the lower Argilliti di Riva di Solto Formation (AdS1), Ponte Giurino village (about 15 km north of Bergamo town), Imagna Valley, Lombardy Basin, Bergamasc Prealps, Northern Italy.

Etymology: After the province of the type locality.

Diagnosis: Same as diagnosis of the genus.

Description:

Holotype specimen no. [6678] labelled [Museo Civico di Scienze Naturali «Enrico Caffi» - Bergamo / E S. 741 Pos. Paratipo / Insecta. Odonata. / Italophlebia gervasuttii,

Whalley 1986. / Età Triassico sup. Norico / Loc. P. te Giurino. / Paleontologia Bergamasca]

An isolated and rather poorly preserved wing, with the postero-basal part missing; the described details of the venation can only be discovered by a very careful examination with a binocular microscope under extreme side-light; the cross-venation is only preserved between costal margin and RP; the wing is about 42.4 mm long, and has a width of 6.7 mm in the postnodal part of the wing; distance between base and nodus, 13.8 mm; distance between nodus and pterostigma, 22.9 mm; the shape of the wing is very elongate and narrow; the costal margin and the hind margin are parallel along most of the postnodal part of the wing; there three antenodal crossveins between costal margin and ScP; there are four crossveins between ScP and RA basal of the nodus; the most distal of these crossveins is obliquely slanted towards the nodus (probably homologous to the nodal veinlet); arculus 0.6 mm distal of the second antenodal crossvein; the nodus is indistinct, without obvious nodal and subnodal veinlets; there are 16 postnodal crossveins visible between the nodus and the pterostigma, but there were probably one or two more of them; the most basal postnodal crossvein is directly at the nodus (point of fusion of ScP with the costal margin); the postnodal crossveins are not aligned with the corresponding crossveins between RA and RP; between RA and RP there are 19 crossveins between the arculus and the stigmal brace; the pterostigma is relatively short and broad (max. 3.3 mm long and max. 1.0 mm wide); the pterostigma seems to be braced by an oblique crossvein aligned with its basal side, and there is only one crossvein beneath it; ScP and RA are basally very close (looking like being fused); IR1 is long and basally fused with RP2, 8.4 mm distal of the midfork; RP2 is distally forked into RP2a and RP2b; IR2 is fused with RP2; IR1, RP2, and IR2 have a common stem fused to RP3/4; the first fork (midfork) of RP is 1.1 mm distal of the nodus; IR1, RP2b, IR2, and the distal part of RP3/4 have a secondary origin on the straight RP-vein that is formed by the basal part of RP3/4, RP2 and RP2a; there is no furcation of RP3/4 preserved, but it might have been present; RP3/4 and MA are strictly parallel and curved towards the hind margin; MP is parallel to MA, so that the postdiscoidal area is very narrow; there could still be a long vein CuA, but the short preserved part could also be a secondary vein as in some other Protomyrmeleontinae; the discoidal cell is basally open (posterior part of arculus absent); there seems to be an oblique vein MAb as distal side of the discoidal cell (artefact ?).

Discussion: The following synapomorphies clearly identify this fossil as an Archizygoptera - Protomyrmeleontidae: IR1 basally fused to RP2; RP2 secondarily forked; MA and RP3/4 distinctly curved towards the posterior wing margin, so that both veins are distinctly shortened. The basal fusion of IR1, RP2 and IR2, which have a common stem on RP3/4, is a strong synapomorphy with the Protomyrmeleontinae (the common stem still originates on RP1/2 instead of RP3/4 in the most basal genus *Malmomyrmeleon* Martínez-Delclòs & Nel 1996), since this character is plesiomorphic in Triassagrioninae, in which IR2 originates on RP3/4, while IR1 and RP2 have common origin on RP1/2. The fusion of IR2 with RP3/4 is an autapomorphy of Triassagrioninae, while the fusion of IR2 with RP2 is an alternative autapomorphy of Protomyrmeleontinae. The following characters seem to differ from all other Protomyrmeleontidae: The pterostigma seems to be braced (a braced pterostigma is

otherwise only known from crown-group Odonata, but unknown from all Protozygoptera and Archizygoptera); IR1 is straight (basally zigzagged in *Triassagrion* and totally zigzagged in the other genera, except *Malmomyrmeleon* Martínez-Delclòs & Nel 1996); RP2b is parallel to RP2a (while parallel to IR2 in all other genera); the distal discoidal vein MAb seems to be oblique (transverse in all other genera). However the referring area of the wing is so poorly preserved that these unusual character states cannot be regarded as certain, since they might partly be artefacts, and therefore should not form the base of evolutionary or phylogenetic hypotheses. An uncontroversial remarkable feature is the large size of the wing, since the other Protozygoptera and Archizygoptera are small insects, except *Malmomyrmeleon* Martínez-Delclòs & Nel 1996 with a wing length of about 47 mm.

unnamed new genus and species
(in Odonata *incertae sedis*)
figures 11-12

Material: Specimen no. [9499a,b], Museo Civico di Scienze Naturali «Enrico Caffi», Bergamo, Italy. No further specimens known yet.

Horizon and locality: Upper Triassic, Upper Norian or Rhaetian, bituminous shales of the lower Argilliti di Riva di Solto Formation (AdS1), Ponte Giurino village (about 15 km north of Bergamo town), Imagna Valley, Lombardy Basin, Bergamasc Prealps, Northern Italy.

Diagnosis and Description:

Specimen no. [9499a,b] labelled [S. 1562 Liv. 35 Nov. 93 / Libellula „Anisozygoptera" inc. sed.]

Part and counterpart of a tiny dragonfly. Only the outline of three wings, head, thorax and the basal abdominal segments is preserved, but no details of the wing venation are visible. Due to the poor state of preservation the only diagnostic characters are the tiny size and the characteristical shape of the wings (figures 11-12), which are only about 16 mm long and hardly stalked. Both wing pairs have a similar shape. The combination of these three characters is unique among the known fossil odonates.

Discussion: Since there are not sufficient characters preserved in the holotype it is currently impossible to attribute this species to any of the subgroups of Odonata. Therefore it has to be regarded as an Odonata *incertae sedis* until better preserved material is available. The specimen should only become the holotype of a new genus and species if no better preserved material should be discovered, simply to avoid the risk to create a nomen dubium.

OTHER TRIASSIC ODONATOPTERA.

Totally 51 different species of Triassic odonatoids are currently known from the following localities, plus about 26 undescribed odonatoid species from the Molteno Formation of South Africa (Anderson pers. comm.) and two new Protomyrmeleontidae from the Triassic of Australia and Russia (NEL pers. comm.):
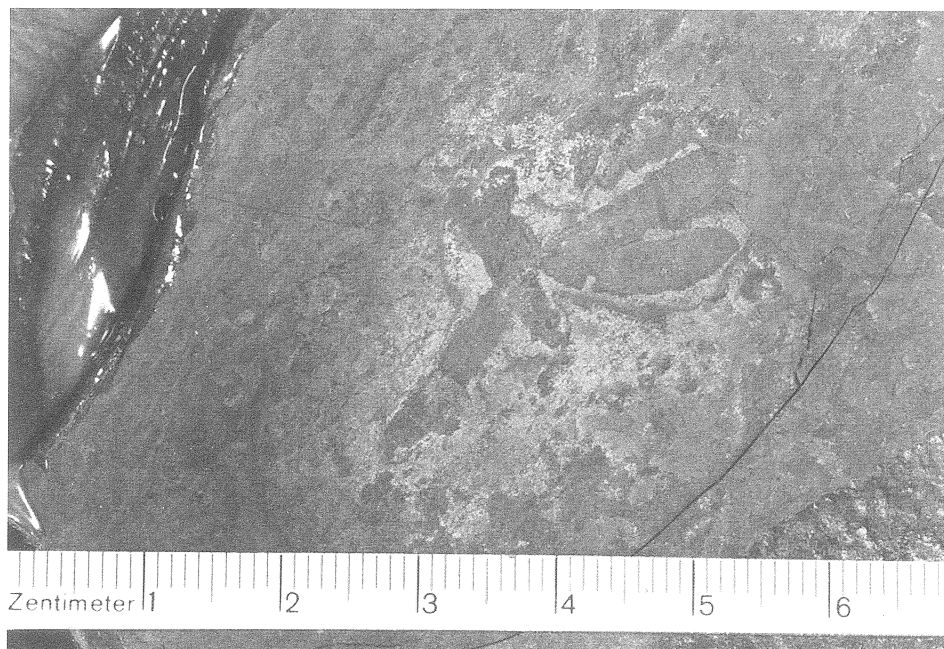
Fig. 11 - Photo of unnamed new genus and species (no. 9499a; part).
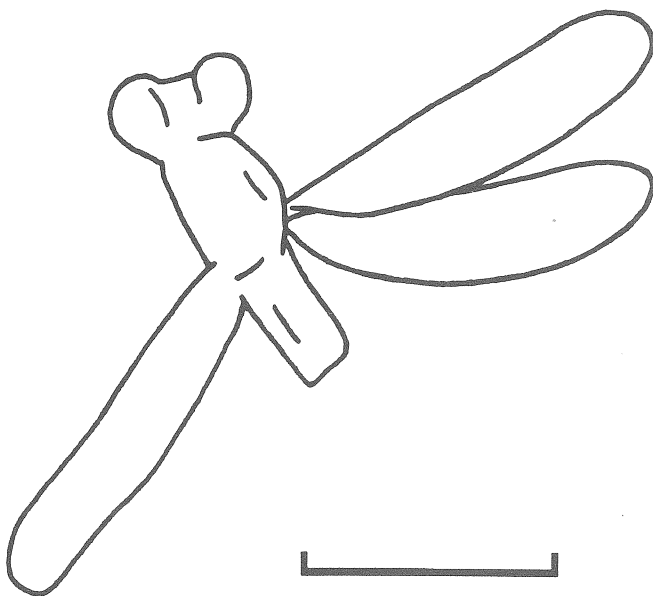
Fig. 12 - Drawing of unnamed new genus and species (no. 9499a; part; scale 10 mm).

Vosges Mts., France; *Voltzia*-sandstone, Lower Triassic, Upper „Buntsandstein":

1.) *Voltzialestes triasicus* Nel *et al*. 1997

Nel *et al*. (1997) regard *Voltzialestes* as a Protozygoptera which shall be closely related to *Triassolestodes*, *Terskeja* and *Batkenia*. This hypothesis is partly confirmed by Bechly (1996) who attributed these genera (except *Triassolestodes*) to the Protomyrmeleontoidea - Batkeniidae within Protozygoptera - Archizygoptera (*sensu* Bechly).

2.) *Reisia gelasii* (Reis 1909) (= *Triadotypus guillaumei* Grauvogel & Laurentiaux 1952a, new synonymy)

Grauvogel & Laurentiaux (1952a,b) and Pritykina (1981) regarded Triadotypidae as members of the protodonate grade. Carpenter (1992) and Bridges (1994) included Triadotypidae in Triadophlebiomorpha. According to Bechly (1996) the Triadotypomorpha (Triadotypidae and Piroutetiidae Nel 1989) constitute the sister-group of Triadophlebiomorpha, forming the monophylum Triadophlebioptera.

Münnerstadt, Lower Franconia, Germany; „Schaumkalk", Middle Triassic, Lower „Muschelkalk":

Reisia gelasii (Reis 1909)

Reis (1909) described *Handlirschia gelasii* of which the genus name is a junior homonym of *Handlirschia* Kohl 1896. Handlirsch (1912) therefore erected the substitute genus *Reisia*. Grauvogel & Laurentiaux (1952b) synonymised *Reisia gelasii* (Reis 1909) with *Triadotypus guillaumei* Grauvogel & Laurentiaux 1952a, but did not consider the correct taxonomical consequences. *Reisia* was placed by Reis (1909) and Handlirsch (1912, 1920) in „Protodonata", and by Carpenter (1931, 1992) in Palaeoptera *incertae sedis*, while Bridges (1994) did not mention this genus at all. I preliminarily agree with the synonymy of *Reisia gelasii* (REIS 1909) with *Triadotypus guillaumei* Grauvogel & Laurentiaux 1952a and therefore recognise the senior synonym *Reisia gelasii* (Reis 1909) as valid name for this genus and species. According to Art. 40(a) IRZN the family-group name Triadotypidae does not have to be changed in this case, although the name of the type-genus changed.

A second alleged protodonate from the Lower Triassic of Germany was described by Kuhn (1937) as *Thuringopteryx gimmi* from the *Chirotherium*-sandstone (Middle „Buntsandstein") of Saalfeld in Thüringen / Eastern Germany. This species was also regarded as Protodonata (probably new family) by Müller (1965), although it had already been transferred to Ensifera *incertae sedis* (possibly belonging to Haglidae) by Zeuner (1939), followed by Carpenter (1992). According to the better illustrations in the redescription by Müller (1965) the attribution to Ensifera has to be rejected, because of the long unbranched veins ScP, RA and RP1. It is also certainly neither an Odonatoptera nor an Ephemeroptera, since the intercalary veins IR1 and IR2 are absent. The wing venation identifies *Thuringopteryx* as a Palaeodictyoptera, probably related to Spilapteridae. This is quite remarkable, since previously there were no Triassic palaeodictyopteroids known at all, and the whole group was believed to have suffered extinction in the Permian.

Dent de Villard (Savoie), Vanoise, France; Middle Triassic, „Keuper":

3.) *Reisia nana* spec. nov.
Grauvogel & Laurentiaux (1952b) described an alleged second specimen of *Triadotypus guillaumei* Grauvogel & Laurentiaux 1952a from this locality. Because of the significant smaller size they called it „forme *nana*". I disagree with the authors that a size difference of one-third of the total wing length is without systematic relevance. I therefore here elevate the „forme *nana*", which has to be regarded as an infrasubspecific taxon according to Art. 45(g)(ii)(1) IRZN, to a new species *Reisia nana* sp. nov. (holotype: École nationale supérieure des Mines de Paris, Salle A, vitrine 9; description and figure: See Grauvogel & Laurentiaux 1952b). According to Nel (pers. comm.) the holotype might now be stored in the collections of the University of Lyon.

Ipswich, Queensland, Australia; Upper Triassic, Carnian (Denmark Hill and Mt. Crosby) and Rhaetian (Brassal Quarry):

4.) *Triassagrion australiense* Tillyard 1922
Triassagrion was classified by Tillyard (1922, 1923) in a separate family Triassagrionidae, that was later synonymised with Protomyrmeleontidae by Fraser (1957), Carpenter (1992) and Bridges (1994). This family group taxon was again restored by Bechly (1996) as subfamily within Protomyrmeleontidae, forming the sister-group to all the other genera of the family (Protomyrmeleontinae). It is also the oldest known member of Protomyrmeleontidae yet.

5.) *Triassolestes epiophlebioides* Tillyard 1918
This species was originally described in a new subfamily of Lestidae by Tillyard (1918), which was elevated to a separate family Triassolestidae by Tillyard (1923). Handlirsch (1939) regarded Triassolestinae as a subfamily of Mesophlebiidae. Carpenter (1992) and Bridges (1994) classified *Triassolestes*, together with *Triassolestodes* and *Triassothemis* in the family Triassolestidae in „Anisozygoptera", while Bechly (1996) again restricted the family Triassolestidae to the type genus and regarded it as possibly the most basal representative of Caloptera (like Fraser 1957) and thus as the oldest known crown-group Zygoptera (like Rozelfelds 1985). However this fossil species is indeed a member of the „anisozygopteroid" grade and is here transferred to Parazygoptera. Pritykina (1981) had already synonymised Mesophlebiidae, Progonophlebiidae, Triassoneuridae, Triassothemistidae with Triassolestidae, in which she included the seven genera *Triassolestes*, *Triassophlebia*, *Mesophlebia*, *Progonophlebia*, *Triassoneura*, *Triassothemis* and *Triassolestodes*. This grouping was rejected by Nel *et al.* (1993), but is strongly confirmed by the present study.

6.) *Mesophlebia antinodalis* Tillyard 1916 (= *Mesophlebia tillyardi* Handlirsch 1939, synonymised by Cowley 1942)
Mesophlebia was originally described in Anisoptera (with question-mark) by Tillyard (1916), but was later transferred by the same author to „Anisozygoptera" (Tillyard 1922, 1923). In Tillyard (1922) *Mesophlebia* actually was cited under Archizygoptera, but this was certainly only a lapse since *Triassagrion* is cited in the same publication as „Anisozygoptera", thus the two names were obviously confused. Fraser (1957), Hennig

(1981) and Rozefelds (1985) also endorsed the placement in „Anisozygoptera", but the genus was afterwards regarded as Odonata *incertae sedis* by Carpenter (1992) and Bridges (1994). Nel *et al.*(1993) and Bechly (1996) regarded *Mesophlebia* as an Odonatoptera *incertae sedis* too, while it is here transferred to Parazygoptera, as sister-genus of *Progonophlebia*.

7.) *Triassophlebia stigmatica* Tillyard 1922

Classified in Mesophlebiidae by Tillyard (1922, 1923) (followed by Fraser 1957), but later regarded by Carpenter (1992) and Bridges (1994) as an „Anisozygoptera" *incertae sedis*, possibly related to *Triassolestes*, while Rozefelds (1985) and Nel *et al.*(1993) regarded *Triassophlebia* as an Odonatoptera *incertae sedis*. The genus is here regarded as a Stigmoptera (*sensu* Bechly 1996) *incertae sedis*, although it is quite possible that this species belongs to Parazygoptera too.

8.) *Perissophlebia multiseriata* Tillyard 1918

Perissophlebia was placed in Odonata *incertae sedis* by Tillyard (1918, 1923), Pritykina (1981), and Rozefelds (1985). It was even regarded as a Palaeoptera *incertae sedis* by Carpenter (1992). The genus is here regarded as an Odonatoptera - Stigmoptera (*sensu* Bechly 1996) *incertae sedis*, because of the odonatoid-like pattern of the main longitudinal veins, the polyneural cross-venation, and the presence of a pterostigma. Quite unique autapomorphies of this genus are the very oblique distal margin of the pterostigma, and the presence of more than one row of cells between the costal margin and RA and between RA and RP distal of the pterostigma. The dense venation might be correlated with the probable very large total size of the wing.

9.) „*Samarura*" *spec. sensu* Rozefelds 1985

I agree with Rozefelds (1985) that this larva might represent the oldest known true Zygoptera, since it has three caudal gill lamellae which could represent an autapomorphy of Zygoptera according to Bechly (1996).

Two further alleged odonates have been described from this locality: *Austrolestidion duaringae* Tillyard 1916, that was described as „two damselfly larvae", turned out to be a single crustacean (Rozefelds 1985); and *Aeroplana mirabilis* Tillyard 1918 that was described in a new family and suborder of „Protodonata". Tillyard (1923) elevated Aeroplanoptera to a separate order, but *Aeroplana* was later generally considered to be a Phasmatodea (Martynov 1928, Riek 1956, Carpenter 1992).

Antitaxineura anomala Tillyard 1935 has erroneously been indicated to be of Triassic age in Carpenter (1992) although it was described from the Upper Permian of New South Wales. The latter species was regarded as Odonata *incertae sedis* by Carpenter (1992) and Bridges (1994), but shall represent a Plecoptera according to Riek in Rozefelds (1985).

Riek (1955) mentions two undescribed and very fragmentary fossil odonates from the Triassic beds of Mt. Crosby in Queensland.

Recently a new protomyrmeleontid was discovered from the Middle Triassic Hawkesbury Sandstone of Beacon Hill in Australia (NSW) and will be described as *Tillyardomyrmeleon petermilleri* gen. et spec. nov. in Henrotay & Nel & Jarzembowski (in print).

Karoo Basin (especially Birds River), South Africa; Molteno Formation, Upper Triassic, Carnian:

According to Anderson (pers. comm.) there are totally 3 genera with 8 species of „protodonates" (19 specimens) and 8 genera with 22 species of „true" odonates (91 specimens) meanwhile known from the Molteno Formation in South Africa. Only the four species listed below have been described yet, while the rest of this promising material will be described by the author for the forthcoming monograph on the fossils of the Molteno Formation.

10.) *Triassologus biseriatus* Riek 1976

Carpenter (1992) and Bechly (1996) used the incorrect subsequent spelling *Triadologus* for *Triassologus*. *Triassologus* was placed by Riek (1976) and Bridges (1994) in Meganisoptera - Paralogidae and by Pritykina (1981) in Odonata, while Carpenter (1992) regarded this genus as a Palaeoptera *incertae sedis*. Bechly (1996) transferred *Triassologus* to the Triadophlebiomorpha - Triadophlebioidea.

The wing venation was probably incorrectly interpreted by Riek (1976): His vein MA indeed rather seems to be IR2, his first branch of Rs (= RP3/4) seems to be RP2 that is secondarily forked into RP2a and RP2b (synapomorphy with Triadotypomorpha and Triadophlebiomorpha *sensu* Bechly 1996), and his second branch of Rs (= RP2) consequently should be IR1. After Riek's interpretation RP3/4 would be forked, which never occurs in Meganisoptera and thus would even contradict his own placement of *Triassologus* in Paralogidae. Furthermore IR2 would be completely absent which never occurs in Odonatoptera. The oblique vein between RA and RP1 is a synapomorphy with Triadophlebioidea (*sensu* Bechly 1996). Since *Triassologus* and *Reisia* (= *Triadotypus*) both have to be regarded as members of Nodialata - Triadophlebioptera (*sensu* Bechly 1996), there are actually no surviving members of the protodonate grade known from the Triassic.

11.) *Triassoneura andersoni* Riek 1976

Triassoneura (Triassoneuridae) was described in Protozygoptera by Riek (1976), which was still endorsed by Fujiyama (1991). Carpenter (1992) and Bridges (1994) regarded *Triassoneura* as „Anisozygoptera" *incertae sedis*. Bechly (1996) regarded Triassoneuridae as Odonata *incertae sedis*, while it is here transferred to the new clade Parazygoptera within Isophlebioptera.

12.-13.) „*Triassoneura*" *heidiae* Riek 1976 and „*Triassoneura*" *regularis* Riek 1976

Both species are here transferred to a new subgenus (*Afrotriassothemis* subgen. nov.) of *Triassothemis*.

Mendoza, Argentina; Late Triassic:

14.) *Triassothemis mendozensis* Carpenter 1960

Carpenter (1960) regarded *Triassothemis* as an Odonata *incertae sedis*. Pritykina (1981), Carpenter (1992) and Nel *et al.* (1993) classified *Triassothemis*, together with *Triassolestodes* and *Triassolestes*, in the family Triassolestidae in „Anisozygoptera" (but in Odonatoptera *incertae sedis* by Nel et al.). Fujiyama (1991) erected a new family Triassothemidae which he believed to be „a link between Permian incipient odonates and modern odonates". Bridges (1994) classified Triassothemistidae in

„Anisozygoptera". Bechly (1996) synonymised Triassothemidae with Triassoneuridae (*sensu* Bechly).

Ominé Coal Field, Miné, Yamaguchi, Japan; Upper Triassic, Carnian:

15.) *„Triassothemis" nipponensis* Fujiyama 1991

16.) *„Triassothemis" minensis* Fujiyama 1991

17.) *„Triassoneura" okafujii* Fujiyama 1991

Bechly (1996) attributed *„Triassothemis" nipponensis* and *„Triassoneura" okafujii* to Progonophlebiidae (*sensu* Bechly). All three species are here transferred in a new genus (*Pseudotriassothemis* gen. nov.) and subfamily (Pseudotriassothemistinae subfam. nov.) within Cyclothemistidae.

Dzhailoycno and Madygen, South Fergana, near Shurab, Batkensk region, Kirghizia (ex U.R.S.S.); Madygen series, Upper Triassic, Norian:

18.) *Kennedya carpenteri* Pritykina 1981

19.) *Kennedya gracilis* Pritykina 1981

20.) *Batkenia pusilla* Pritykina 1981

21.) *Terskeja paula* Pritykina 1981

22.) *Terskeja pumilio* Pritykina 1981

23.) *Terskeja tenuis* Pritykina 1981

24.) *Reisia sogdianus* (Pritykina 1981) comb. nov.

This species was originally described in the genus *Triadotypus* Grauvogel & Laurentiaux 1952a which has to be regarded as a junior subjective synonym of *Reisia* Handlirsch 1912 (see above).

25.) *Triassolestodes asiaticus* Pritykina 1981

Triassolestodes was generally classified in Triassolestidae (Pritykina 1981; Carpenter 1992; Nel *et al.* 1993; Bridges 1994). Bechly (1996) recognised the close relationship of *Triassolestodes* and *Triassoneura*, but erroneously excluded *Triassolestes* from this group.

26.) *„Triassoneura" primitiva* Pritykina 1981

„Triassoneura" primitiva is here transferred to Archizygoptera - Batkeniidae, because its venation is extremely similar with that of *Batkenia* Pritykina 1981. This new position implicates the erection of a new genus *Paratriassoneura* gen. nov. (type species: *„Triassoneura" primitiva* Pritykina 1981; description: See Pritykina 1981; autapomorphies: Origins of RP2 and IR2 separated by six cells).

27.- 46.) all twenty species of **Triadophlebiomorpha** *sensu* Pritykina 1981

Except *Triassolestodes* all mentioned taxa from this locality belong to the stem-group of Odonata. *Kennedya*, *Terskeja* and *Batkenia* clearly are Protozygoptera (Bechly 1996), just like *„Triassoneura" primitiva* too (the latter species was erroneously attributed to the genus *Triassolestodes* by Bridges 1994). Triadotypidae belongs to the sister-group of Triadophlebiomorpha (see above). A new phylogenetic system of Triadotypidae, Triadophlebiomorpha, and Protozygoptera has been proposed by Bechly (1996) and is not repeated here. *Terskeja* was described by Pritykina (1981) in the family Protomyrmeleontidae, but regarded by Carpenter (1992) and Bridges (1994) as an Archizygoptera (*sensu* Carpenter; = „Protozygoptera" & Archizygoptera auct.)

incertae sedis. Nel & Henrotay (1992) regarded *Terskeja* as an Odonatoptera *incertae sedis.* Nel *et al.* (1997) regarded *Terskeja* as a Protozygoptera, closely related to *Batkenia* and *Voltzialestes.* This hypothesis fully agrees with Bechly (1996) who transferred these three genera to the Protomyrmeleontoidea - Batkeniidae within Protozygoptera - Archizygoptera (*sensu* Bechly).

Nel (pers. comm.) recently found a new genus and species of Protomyrmeleontidae from the Triassic of Russia (description in prep.).

Ponte Giurino, Lombardy, Italy; Lower Argilliti di Riva di Solto Formation, Upper Triassic, Upper Norian or Rhaetian:

These four taxa are described in detail within this paper.

47.) *Italophlebia gervasuttii* Whalley 1986

48.) *Italophlebia paganoniae* spec. nov.

49.) *Italomyrmeleon bergomensis* gen. et spec. nov.

50.) unnamed new genus and species

Shurab, Fergana, Isfara district, Tadzhikistan, Central Asia (ex U.R.S.S.); Upper Triassic, Rhaetian:

51.) *Sogdophlebia singularis* Pritykina 1970

Originally described in Heterophlebiidea - Liassophlebiidae (*sensu* Pritykina), but transferred to Isophlebioidea - Campterophlebiidae by Nel *et al.* (1993). This placement is also endorsed here. The Rhaetian age could be doubtful, since this species was indicated as of Jurassic age by Carpenter (1992) (or is this just a lapsus ?).

PHYLOGENETIC SYSTEM OF PARAZYGOPTERA (FIGURE 13). As recently suggested by Cantino *et al.* (1997), for each taxon a phylogenetic definition, a list of the referring autapomorphies (the synapomorphies of its members) and a list of the currently known members of the taxon is provided. All given phylogenetic definitions are stem-based. Categorial ranks have been avoided as far as possible, and the hierarchical subordination of taxa is therefore indicated by a corresponding indention.

<center>Parazygoptera taxon nov.</center>

Phylogenetic definition: The most inclusive clade that contains *Asiopteron antiquum* Pritykina 1968 and *Italophlebia gervasuttii* Whalley 1986 but neither *Isophlebia aspasia* (Hagen 1862) nor any of the other type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: RP2 arising distinctly distal of subnodus (only reversed in *Cyclothemis sagulica* Pritykina 1980).

The petiolation of the hind wing most probably represents a plesiomorphy, since this state is also present in Campyloptera, Triadophlebiomorpha, Protozygoptera, Zygoptera, Tarsophlebioptera, Epiophlebioptera, Heterophlebioptera and Stenophlebioptera. The secondary loss of the lestine-oblique-vein in many Parazygoptera is clearly due to a multiple convergence (since this veinlet is retained in *Mesoepiophlebia, Ensphingophlebia, Cyclothemis* and *Shurabiola,* and maybe also in

Pseudotriassothemis and *Mesophlebia*), probably caused by the shifting of the origin of RP2 distal of the subnodus, as a pre-disposition.

Membership: Including Sphenophlebiidae fam. nov. and the sister-groups Asiopteridae and Triassolestoidea (Euparazygoptera). *Triassophlebia stigmatica* Tillyard 1922 could be a member of Parazygoptera too, but this is very uncertain because of the fragmentary state of the holotype.
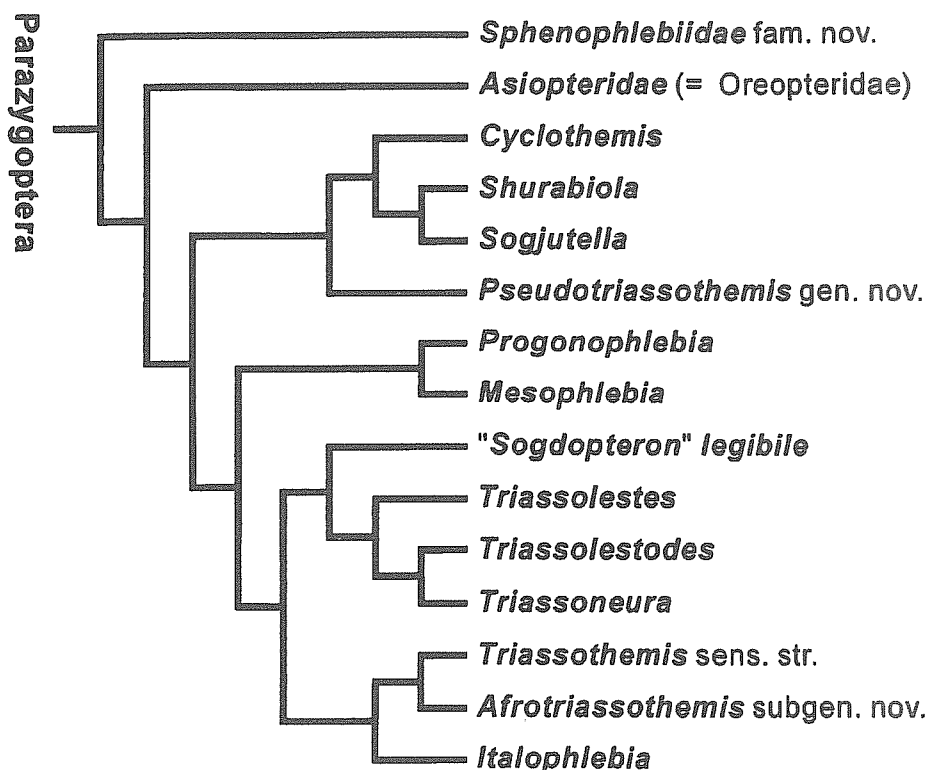

Fig. 13 - Phylogenetic tree of Parazygoptera taxon nov.

Sphenophlebiidae fam. nov.

Type genus: *Sphenophlebia* Bode 1953.

Phylogenetic definition: The most inclusive clade that contains *Sphenophlebia interrupta* Bode 1953 but neither *Asiopteron antiquum* Pritykina 1968 nor *Triassolestes epiophlebioides* Tillyard 1918 or any of the type-species of the type-

genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: Several long intercalary veins between IR1 and RP1, and between IR1 and RP2, as well as between RP3/4 and IR2, and between IR2 and RP2 (convergent to *Erichschmidtia* and *Euthemis*).

Membership: Including *Sphenophlebia interrupta* Bode 1953, *Mesoepiophlebia veronicae* Nel & Henrotay in Nel *et al.* 1993 and *Ensphingophlebia undulata* Bode 1953. *Proeuthemis pritykinae* Nel & Jarzembowski 1996 most probably also belong to this new family, although its zigzagged MA agrees with Asiopteridae. However the similar derived pattern of intercalary veins is here preliminarily regarded as the stronger evidence.

Euparazygoptera taxon nov.

Phylogenetic definition: The most inclusive clade that contains *Asiopteron antiquum* Pritykina 1968 and *Italophlebia gervasuttii* Whalley 1986 but neither *Sphenophlebia interrupta* Bode 1953 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: No antefurcal crossveins present in the space between RP and MA basal of the midfork (only reversed in *Italophlebia gervasuttii*).

Membership: Including the sister-groups Asiopteridae and Triassolestoidea.

Asiopteridae Pritykina 1968 *sensu nov.*

(= Oreopteridae Pritykina 1968, new synonymy; = Oreopteroidea *sensu* Nel *et al.* 1993; = Metazygoptera *sensu* Lohmann 1981)

Phylogenetic definition: The most inclusive clade that contains *Asiopteron antiquum* Pritykina 1968 but neither *Triassolestes epiophlebioides* Tillyard 1918 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: IR2 distally zigzagged (convergent to „*Sogdopteron*" *legibile*); MA distally zigzagged (convergent to Steleopteridae, Mesophlebiinae, and *Italophlebia*); hind wing discoidal cell secondarily more quadrangle-like, thus with an oblique distal side MAb (reversal; convergent to *Sogjutella mollis*).

Membership: All genera formerly included in Oreopteridae Pritykina 1968 and Asiopteridae *sensu* Pritykina 1968. Two further members are „*Mesoepiophlebia*" *bexleyi* Nel & Jarzembowski 1996 and „*Sphenophlebia*" *pommerana* Ansorge 1996 which is here transferred to the genus *Turanopteron* Pritykina 1968 because of the nearly identical venation that was already recognised by Ansorge (1996). *Oreopteron asiaticum* Pritykina 1968 and *Oreopterella paula* Pritykina 1968 seem to be closely related, since they uniquely share a zigzagged RP1, while „*Oreopteron*" *simile* Pritykina 1968 has to be transferred to the genus *Asiopteron* Pritykina 1968. Since Oreopteridae and the genus *Oreopteron* are not monophyletic, and Asiopteridae lacks any autapomorphies if Oreopteridae are excluded, Oreopteridae is here regarded as a synonym of Asiopteridae. A detailed phylogenetic system of Asiopteridae and several new genera and species will be introduced in Nel *et al.* (in prep.). Carle & Wighton

(1990: 58) suggested that Oreopteridae and Asiopteridae are synonyms of Progonophlebiidae, although they did not justify this hypothesis, which has to be rejected according to the present study (also see Nel *et al.*, 1993).

Triassolestoidea Tillyard 1918 sens. nov.
(= Progonophlebioidea *sensu* Bechly 1996)

Phylogenetic definition: The most inclusive clade that contains *Triassolestes epiophlebioides* Tillyard 1918 but neither *Oreopteron asiaticum* Pritykina 1968 nor *Isophlebia aspasia* (Hagen 1862) or any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).
Autapomorphies: Nodal and subnodal veinlet not aligned and separated by a short kink in RA (unique within Odonata, but further transformed in Triassolestinae).
Membership: Including the sister-groups Cyclothemistidae and Triassolestidae.

Cyclothemistidae Bechly 1996

Phylogenetic definition: The most inclusive clade that contains *Cyclothemis sagulica* Pritykina 1980 but neither *Triassolestes epiophlebioides* Tillyard 1918 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).
Autapomorphies: The typical pattern of the longitudinal veins in Isophlebioptera is reversed (convergent to Selenothemistidae; certainly not a symplesiomorphy), so that the postdiscoidal space is not narrowed distally, and the space between RP3/4 and MA is less expanded (RP3/4 is even parallel to MA in *Cyclothemis*).
Membership: Including   the   sister-groups   Cyclothemistinae   and Pseudotriassothemistinae subfam. nov.

Cyclothemistinae Bechly 1996 stat. nov.

Phylogenetic definition: The most inclusive clade that contains *Cyclothemis sagulica* Pritykina 1980 but neither *Pseudotriassothemis nipponensis* (Fujiyama 1991) nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).
Autapomorphies: Cubito-anal area and posterior branches of CuAa strongly reduced. *Shurabiola* and *Sogjutella* share the complete suppression of all secondary antenodal and all antesubnodal crossveins as putative synapomorphies.
Autapomorphies of *Sogjutella* are the oblique vein MAb (reversal), the suppression of the lestine oblique vein between RP2 and IR2, and the strongly reduced anal and cubito-anal area in the hind wing, with only one row of cells, which is correlate with the generally reduced venation and the slender shape of the wing.
Membership: Only including the two species of *Cyclothemis* Pritykina 1980, and the mono-specific sister-genera *Shurabiola* Pritykina 1980 and *Sogjutella* Pritykina 1980. *Sogjutella* is certainly no member of Asiopteridae (= Oreopteridae), since it shares the unique kink in RA between nodal and subnodal veinlet as strong synapomorphy with Triassolestoidea.

Pseudotriassothemistinae subfam. nov.

Type genus: *Pseudotriassothemis* gen. nov. (type species: „*Triassothemis*" *nipponensis* Fujiyama 1991; etymology: In reference to the misleading similarity to the genus *Triassothemis*; autapomorphies: Same as subfamily).

Phylogenetic definition: The most inclusive clade that contains *Pseudotriassothemis nipponensis* (Fujiyama 1991) but neither *Cyclothemis sagulica* Pritykina 1980 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: CuP-crossing looking like an anterior secondary branch of AA (not like a short, straight and transverse „crossvein" but elongated, curved, and more or less parallel to the longitudinal veins), that is ending directly beneath the arculus (at least in hind wings); hind wing with two strongly curved basal posterior branches of AA (unique within Odonatoptera); IR2 originating on RP3/4; at least the hind wings are secondarily non-petiolated; hind wing nodus in a very basal position.

P. okafujii and *P. nipponensis* at least are sister-species (synapomorphy: Unique crossvein-brace between RP and IR2 below the subnodus) or might even represent fore and hind wing of the same species, but this could only be positively demonstrated if a specimen with both wing pairs preserved together would be found. An autapomorphy of *P. minensis* seems to be the secondary presence of secondary antenodals between costal margin and ScP distal of Ax2 (convergent to Mesophlebiinae and *Italophlebia*).

Membership: Including the former taxa „*Triassoneura*" *okafujii* Fujiyama 1991, „*Triassothemis*" *nipponensis* Fujiyama 1991 and „*Triassothemis*" *minensis* Fujiyama 1991.

Triassolestidae Tillyard 1918 (*sensu* Pritykina 1981)

Phylogenetic definition: The most inclusive clade that contains *Triassolestes epiophlebioides* Tillyard 1918 but neither *Cyclothemis sagulica* Pritykina 1980 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: In the hind wing [AA & CuP] and [MP & CuA] are partly fused basal of the arculus (quite unique within Odonata; currently known from *Progonophlebia*, *Triassolestodes*, „*Sogdopteron*" *legibile*, and *Italophlebia*); in the hind wing the distal part free part of [AA & CuP] is not longitudinal and fusing with CuAa but perpendicular (aligned with arculus) and directed towards the hind margin, so that the subdiscoidal cell is posteriorly open (convergent to Isophlebiidae); characteristical kink in CuA between the „gaff"-portion and CuAb in the hind wing.

Membership: Including the sister-groups Mesophlebiinae and Triassolestinae.

Mesophlebiinae Tillyard 1916 sens. nov.

(= Progonophlebiidae Tillyard 1925, new synonymy)

Phylogenetic definition: The most inclusive clade that contains *Mesophlebia antinodalis* Tillyard 1916 but neither *Triassoneura andersoni* Riek 1976 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: Nodus distal of the midwing position since the postnodal part of the hind wing distinctly shortened (a unique character in the „anisozygopteroid" grade); MA distally zigzagged (convergent to Steleopteridae, Asiopteridae and *Italophlebia*); characteristical shape of the distal furcation of RP into RP1 and RP2 (unsafe in *Progonophlebia*); RP1 and RA at least somewhat converging beneath the pterostigma (unsafe in *Progonophlebia*); secondary presence of secondary antenodals between costal margin and ScP distal of Ax2 (convergent to Pseudotriassothemistinae subfam. nov. and *Italophlebia*, but not certain for *Progonophlebia*, thus maybe rather an autapomorphy of *Mesophlebia*).

Unique autapomorphies of *Mesophlebia* are an oblique vein that is obliquely slanted towards the apex between RP and IR2 below the transverse subnodus, the reversed obliquity of the nodal crossvein (convergent to *Triassolestodes*), and a more distinct constriction of the space between RA and RP1 beneath the pterostigma.

Membership: Only including the two sister-genera *Mesophlebia* Tillyard 1916 and *Progonophlebia* Tillyard 1925. *Progonophlebia cromptoni* Zeuner 1958 (please note the original spelling, not „*cramptoni*" as e.g. in Nel *et al.* 1993) shall be a synonym of *Progonophlebia woodwardi* Tillyard 1925 according to Nel (pers. comm.).

<p style="text-align:center">Triassolestinae Tillyard 1918 sens. nov.</p>

Phylogenetic definition: The most inclusive clade that contains *Triassolestes epiophlebioides* Tillyard 1918 but neither *Mesophlebia antinodalis* Tillyard 1916 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: Fore wing distinctly petiolated (polarity unsafe); nodus and subnodus are perpendicular to RA, and more or less aligned (reversal); somewhat basal of the subnodus there is a distinctly oblique crossvein that is obliquely slanted towards the apex between RA and RP (most distinct in *Triassolestodes asiaticus*, but also clearly present in *Italophlebia gervasuttii* and *Triassothemis mendozensis*); distinctly reduced number of antesubnodal crossveins (only 2 or 3).

Membership: Including the sister-groups Triassolestini and Triassothemistini.

<p style="text-align:center">Triassothemistini Fujiyama 1991 stat. et sens. nov.
(nomen correctum et translatum pro Triassothemidae Fujiyama 1991)
ʾ   (= Italophlebiidae Whalley 1986, new synonymy)</p>

Phylogenetic definition: The most inclusive clade that contains *Triassothemis mendozensis* Carpenter 1961 but neither *Triassoneura andersoni* Riek 1976 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: MA and MP distinctly converging near the hind margin; area between RP3/4 and MA basally rather narrow for a considerable distance; area between IR2 and RP3/4 basally very narrow, then expanded, and distally again narrowed; area between RP2 and IR2 basally very narrow.

Distinct autapomorphies of *Italophlebia* are the distally strongly converging veins RP1 and RP2, the distally zigzagged vein MA, and the shortened and zigzagged IR1.

Membership: Only including the two genera *Italophlebia* and *Triassothemis*. The latter genus also includes the former taxa „*Triassoneura*" *heidiae* Riek 1976 and „*Triassoneura*" *regularis* RIEK 1976, which are here classified in a new subgenus *Afrotriassothemis* subgen. nov. (type species: „*Triassoneura*" *regularis* Riek 1976; etymology: After Africa and the generic name „*Triassothemis*"; autapomorphies: Numerous cells below the elongated pterostigma; very long and straight IR1; RP2 and IR2 basally very close together fore a longer distance; two rows of cells between the distal parts of IR2 and RP3/4), while *Triassothemis mendozensis* Carpenter 1961 is classified in the nominate subgenus *Triassothemis*.

Triassolestini Tillyard 1918 stat. et sens. nov.

Phylogenetic definition: The most inclusive clade that contains *Triassolestes epiophlebioides* Tillyard 1918 but neither *Triassothemis mendozensis* Carpenter 1961 nor any of the type-species of the type-genera of the non-parazygopteran family-group taxa *sensu* Bechly (1996) (stem-based definition).

Autapomorphies: Arculus secondarily shifted closer to Ax2 than to Ax1, or even distal of Ax2 (not preserved in *Triassolestes*).

A strong synapomorphy of all Triassolestini, except the most basal „*Sogdopteron*" *legibile*, is a unique veinal pattern in the fore wing base, in which [AA & CuP] is basally fused with the hind margin, and distally fused with [MP & CuA], only two short portions remained free, the basal one looking like the CuP-crossing, and the distal one as oblique „pseudo-subdiscoidal veinlet" beneath the tip of the discoidal cell (unique within Odonatoptera).

A distinct synapomorphy of *Triassolestodes* and *Triassoneura* is the short basal fusion of MP and CuA distal of the fore wing discoidal cell (unique within Odonatoptera, but similar to the hind wing of Tarsophlebiidae). A further synapomorphy of these two genera might be the circumstance that Ax2 is secondarily shifted basal of the arculus (reversal), but this character is unknown in *Triassolestes*.

The holotypical wing of *Triassolestes* looks very similar to the fore wing of *Triassoneura* and *Triassolestodes*. The only conflicting character would be the closed discoidal cell, but according to Nel (pers. comm.) this character state is based on an error of Tillyard. An unusual feature (autapomorphy) of *Triassolestes* is the distally widened postdiscoidal area with more than one row of cells in the widened part. However such an autapomorphic reversal happened in Cyclothemistidae too.

Autapomorphies of *Triassolestodes* are the reversed obliquity of the nodal crossvein (convergent to *Mesophlebia*), a unique type of hind wing arculus (Nel pers. comm.), and the reduced wing venation with only one row of cells between all the longitudinal veins, giving the wing a zygopteroid appearance. Distinct autapomorphies of „*Sogdopteron*" *legibile* Pritykina 1980 are the basally zigzagged RP2 and the distal obliteration of MA. The distally converging veins MA and MP may be a derived similarity with Triassothemistini, but the position of the arculus closer to Ax2 than to Ax1 has to be regarded as stronger evidence for a relationship with Triassolestini, since this character state is a very rare reversal within Epiproctophora.

Membership: Only including *Triassolestes epiophlebioides* Tillyard 1918, *Triassoneura andersoni* Riek 1976 and *Triassolestodes asiaticus* Pritykina 1981, and probably also „*Sogdopteron*" *legibile* Pritykina 1980, which will be classified in a new genus *Sogdopterites* in Nel *et al.* (in prep.). „*Triassoneura*" *primitiva* Pritykina 1981 is an Archizygoptera that seems to be closely related to the genus *Batkenia* Pritykina 1981.

PHYLOGENETIC POSITION OF PARAZYGOPTERA. Parazygoptera shares with Epiproctophora (Epiophlebiidae and Anisoptera) the following synapomorphies: Arculus shifted basally in a position between the two primary antenodals Ax1 and Ax2; distinct anal angle in male hind wings; costal margin not indented at node, since the costal margin basal of the nodus is in line with the costal margin distal of the nodus instead of being curved on it; adult males with reduced or suppressed paraprocts and development of a secondary epiproctal projection as single appendix inferior; thorax and abdomen are relatively strong and stout.
Parazygoptera shares the following synapomorphies with Euryoptera (Anisoptera and its stem-group): Distal discoidal vein MAb at least less oblique in the fore wing and transverse or even of reversed obliquity in the hind wing; cubito-anal field secondarily expanded in hind wings; secondary branching of the CuA into an antererior longitudinal branch CuAa and a posterior transverse branch CuAb; male hind wings with an anal triangle; complete suppression of the paraprocts in adults.
Parazygoptera is indentified as a member of Isophlebioptera by the following synapomorphies: In hind wings the subdiscoidal cell is enlarged and has a bulged posterior margin, correlated with a unique course of the anal vein AA („pseudo-anal-loop"), which is strongly bent towards the posterior wing margin at the CuP-crossing; RP3/4 rather parallel to IR2, thus the space between RP3/4 and MA is distinctly expanded and traversed by several pektinate convex „secondary branches" of RP3/4; postdiscoidal space between MP and MA very narrow, with only one row of cells between them in the ground-plan; CuAa shortened and postero-distally indistinct (zigzagged), thus the distal space between MP and CuAa strongly expanded; distal of Ax2 all antenodals between the costal margin and ScP are suppressed in the ground-plan.

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INDIRIZZO DELL'AUTORE: Günter BECHLY
                       Institut und Museum für Geologie und Paläontologie
                       Eberhard-Karls Universität Tübingen
                       Sigwartstr. 10
                       D-72076 Tübingen
                       GERMANY
                       (email: GBechly@aol.com)