

The Ephemeroidea (Insecta) from the Grès à Voltzia (early Middle Triassic) of the Vosges (NE France)

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with 11 figures

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Abstract: The study of the Ephemeroidea (385 specimens) of the GRAUVOGEL and GALL collection from the Grès à Voltzia (early Middle Triassic) of the Vosges, NE France, enabled the description of two new genera based on wings and six new genera based on nymphs. The new monotypic wing genera are *Toxodotes coloratus* n. gen. n. sp. (Toxodotidae n. fam.) and *Triassodotes vogesiacus* n. gen. n. sp. (family Misthodotidae SELLARDS). The Misthodotidae, known until now only from the Permian, crossed the Permian/Triassic boundary and did not seem to have been affected by the end-Permian biotic crisis. Apart from the genera based on wings, six new monotypic genera are represented by nymphs only: *Triassoephemera punctata* n. gen. n. sp. (Triassoephemeridae n. fam.); *Voltziaephemera fossoria* n. gen. n. sp. (Voltziaephemeridae n. fam.), the most common species in the Grès à Voltzia; *Triassomanthus parvulus* n. gen. n. sp. (Triassomanthidae n. fam.); *Triassonurus doliiformis* n. gen. n. sp. (family Siphonuridae ULMER), now the oldest record of this family; *Minorella virgata* n. gen. n. sp. (family undetermined); *Vogesonympha ludovici* n. gen. n. sp. (Vogesonymphidae n. fam., Pterygota incertae sedis). Additionally, *Mesopteropteran longipes* (HANDLIRSCH) (family Mesopteropteridae DEMOULIN) which was described earlier, is also present in the GRAUVOGEL & GALL collection. The morphology of the Ephemeroidea nymphs, at least for some of them, enables the interpretation of their probable habitats and life conditions, and thus contributes to our knowledge of the Grès à Voltzia palaeoenvironment.

Keywords: Ephemeroidea • Systematics • Middle Triassic • Buntsandstein • Grès à Voltzia • Vosges • France

Kurzfassung: Die Untersuchung der Ephemeroidea (385 Exemplare) der GRAUVOGEL und GALL Sammlungen aus dem Grès à Voltzia (frühe Mittel-Trias) der Vogesen, NE Frankreich ermöglicht die Aufstellung und Beschreibung von zwei neuen monotypischen Gattungen basierend auf der Flügel-Morphologie und sechs neuen monotypischen Gattungen basierend auf den Nymphen. Die neuen Flügel-Gattungen sind *Toxodotes coloratus* n. gen. n. sp. (Toxodotidae n. fam.) und *Triassodotes vogesiacus* n. gen. n. sp. (Familie Misthodotidae). Die Misthodotidae, bisher nur aus dem Perm bekannt, überschritten die Perm/Trias-Grenze und scheinen von der biotischen Krise am Ende des Perms nicht beeinflusst worden zu sein. Die 6 monotypischen auf Nymphen basierenden Gattungen sind *Triassoephemera punctata* n. gen. n. sp. (Triassoephemeridae n. fam.); *Voltziaephemera fossoria* n. gen. n. sp. (Voltziaephemeridae n. fam.), die häufigste Art im Grès à Voltzia; *Triassomanthus parvulus* n. gen. n. sp. (Triassomanthidae n. fam.); *Triassonurus doliiformis* n. gen. n. sp. (Familie Siphonuridae ULMER), der hiermit älteste Nachweis der Familie; *Minorella virgata* n. gen. n. sp. (Familie unbestimmt); *Vogesonympha ludovici* n. gen. n. sp. (Vogesonymphidae n. fam., Pterygota incertae sedis). *Mesopteropteran longipes* (HANDLIRSCH, 1918) (Familie Mesopteropteridae DEMOULIN), bereits vorher beschrieben, ist in der GRAUVOGEL & GALL Sammlung ebenfalls vertreten. Die Morphologie einiger Ephemeroidea-Nymphen erlaubt die Interpretation ihres möglichen Habitats and ihrer Lebensweise und trägt damit zur Kenntnis der Umweltbedingungen während der Ablagerung des Grès à Voltzia bei.

Schlüsselwörter: Ephemeroidea • Systematik • Mittel-Trias • Buntsandstein • Grès à Voltzia • Vogesen • Frankreich

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Introduction

The paleontological collection GRAUVOGEL and GALL from the Grès à Voltzia of the Vosges Mountains (NE France), which consists of 5300 specimens and about 200 species, shows that the palaeontofauna was very rich and well diversified in the early Middle Triassic, contrary to what is generally thought (MARCHAL-PAPIER 1998: 32, 35). Indeed, most of the insect orders are represented in this collection, particularly the Blattodea (41 %), Coleoptera (12 %), Ephemeroidea (7.3 %), Hemiptera (18 %), Diptera (5.3 %), Orthoptera, Megaloptera, Neuroptera, Mecoptera, Odonoptera, Psocoptera, "Protorthoptera", Trichoptera and Plecoptera.

Several orders have already been studied, such as the Blattodea (PAPIER et al. 1994, 1996a; PAPIER & GRAUVOGEL-STAMM 1995), the Mecoptera (LAURENTIAUX & GRAUVOGEL in LAURENTIAUX 1953; KRZEMINSKI & KRZEMINSKA 1996; PAPIER et al. 1996b), the Diptera (KRZEMINSKI et al. 1994), the Odonata (GRAUVOGEL & LAURENTIAUX 1952; NEL et al. 1996), the Hemiptera (LEFEBVRE et al. 1998) and the Orthoptera (PAPIER et al. 1997, 2000). Likewise, concerning the Ephemeroidea from the Grès à Voltzia, a nymph has already been described by HANDLIRSCH (1918: 112) under the name *Mesoplecteron longipes*.

The present study deals with all the Ephemeroidea present in the GRAUVOGEL and GALL collection which are represented by 385 specimens. They consist of two species based on wings and seven species based on nymphs. The nymphs are far more numerous (93.5 %) than the wings (6.5 %). Since the Ephemeroidea nymphs lived exclusively in freshwater, they contribute to improve our knowledge of the Grès à Voltzia environment.

Up until now the Ephemeroidea from the Triassic were poorly known. The brief survey given by SINITSHENKOVA (in RASNITZYN 2002: 391–392) shows that Ephemeroidea have been reported from the Buntsandstein of Mallorca, Spain (one specimen; CALAFAT-COLOM 1988), the Urals (Bukobay Formation, Anisian), West Siberia (Varengayakha Formation, Anisian) (SINITSHENKOVA 2000: 276), Kirghizistan (Madygen Formation, Ladinian/Carnian) and Ukraine (Carnian/Norian) (SINITSHENKOVA 2000: 276–277). It is noteworthy that in the Madygen Formation, which is the richest Triassic insect locality, only two specimens have been found whereas the Grès à Voltzia, by contrast, has provided a lot of Ephemeroidea. In the Triassic of Gondwanaland, mayflies have been found only in South Africa (Molteno Formation, Carnian) where a nymph called *Litophlebia* was described (RIEK 1976: 149–150). Some further findings of Ephemeroidea were reported from Spain, province Tarragone (VIA & CALZADA 1987: 274), from the Middle/Upper Triassic of Switzerland (KRZEMINSKI & LOMBARDO 2001: 72) and from Germany (Thuringia) by KUHN (1937: 191–192) who described it first as a dragonfly (*Thuringopterix*). Com-

pared to all these records, the Grès à Voltzia of the Vosges (early Middle Triassic, NE France) has provided the most specimens (385) and the highest diversity (9 species) of Ephemeroidea known from the Triassic.

Geographic situation of the fossil localities

The fossil localities of the Grès à Voltzia having afforded Ephemeroidea are all situated in the Northern Vosges Mountains (NE France) (Fig. 1). Among them, Adamswiller and Bust (Bas-Rhin) have yielded respectively 38 % and 14.5 % of the Ephemeroidea specimens. The localities Arzviller, Vilsberg and Hangviller (Moselle) have provided 25 %, 16 % and 1.5 % respectively. The remaining 5 % Ephemeroidea came from other localities (Cocheren, Lutzelbourg in the department of Moselle and Schoenbourg, Petersbach and Gottenhouse in the department of Bas-Rhin).

Repository: All the specimens of the GRAUVOGEL and GALL collection and HANDLIRSCH's specimens studied in the present work are housed at EOST-Géologie, Université Louis Pasteur, 1 rue Blessig, 67084 Strasbourg Cedex, France.

Stratigraphic distribution

The Grès à Voltzia corresponds to the upper part of the Buntsandstein, which represents the upper part of the Lower Triassic with a German facies. However, the age of the Grès à Voltzia from the Vosges Mountains was demonstrated to be early Anisian, which corresponds to the basal part of the Middle Triassic in the Alpine stratigraphy (DURAND & JURAIN 1969: 1049; GALL 1971: 184).

The Grès à Voltzia consists of two units, being from the base to the top:

- the **Grès à meules** has a lenticular stratification and contains terrestrial fossils. The fossil insects come from this unit, particularly from the green silty-clay lenses intercalated between the sandstone beds. The Grès à meules was deposited at the boundary between marine and continental areas, in a deltaic environment consisting of channels and temporary ponds with shallow and more or less brackish water (GALL 1971: 182). The silty-clay lenses correspond to the sediments deposited in the ponds.
- the **Grès argileux** has a horizontal stratification and contains only marine fossils.

Systematic paleontology

The systematic study of the Ephemeroidea from the Grès à Voltzia is based on forewings, hindwings and nymphs, most of which are entire. The coexistence in the Grès à Voltzia of some isolated wings and many nymphs hinted at a connection. However the criteria proposed by SINITSHENKOVA (1987: 86) for determining species have not indicated any relationships between them. Therefore

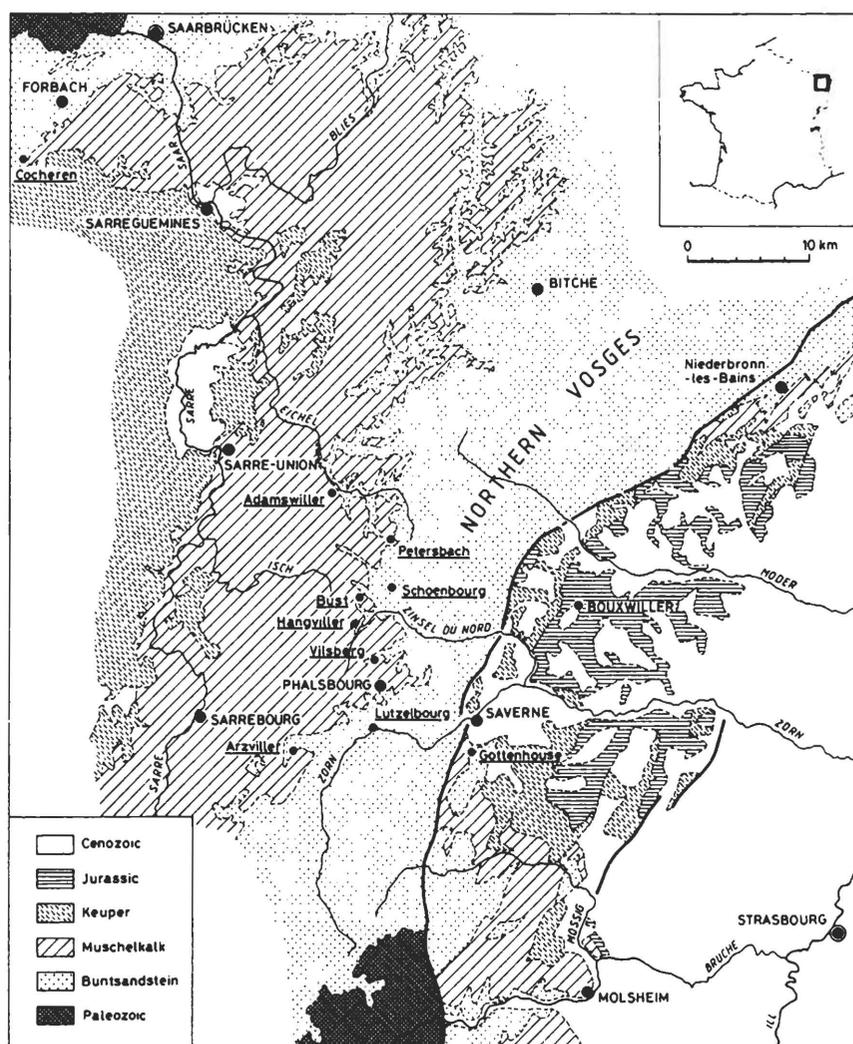


Fig. 1. Geographic distribution of the fossil localities.

the nymphs and wings from the Grès à Voltzia have been attributed to separate taxa.

The criteria for determining the connections between wings and nymphs were first proposed for fossil stoneflies, but these proved to be the same for fossil mayflies. Indeed, judging from living ones, the life cycles of both are very similar. The different criteria which may indicate if the Ephemeroidea nymphs and adults (represented by isolated wings) are conspecific are: the nymphs and adults must occur in the same locality; both nymphs and adults must show features suggesting that they represent the same higher taxon (taxonomic compatibility); and the mature nymphs and adults must be comparable in body size (size compatibility). In the case of the Ephemeroidea from the Grès à Voltzia these conditions are not fulfilled. The nymphs are either too large or too small compared to the size of the wings. Therefore, two new wing taxa (*Triassodotes vogesiacus* n. gen. n. sp. and *Toxodotes coloratus* n. gen. n. sp.) and seven nymph taxa among which six are new (*Vogesonympha ludovici* n. gen. n. sp., *Triassoephemera punctata* n. gen. n. sp., *Triassomanthus parvulus* n. gen. n. sp., *Triassonurus doliiformis* n. gen. n. sp., *Minorella virgata* n.

gen. n. sp., *Voltziaephemera fossoria* n. gen. n. sp.) are proposed, along with a redescription of *Mesoplectopteron longipes* HANDLIRSCH, 1918.

Class Insecta LINNAEUS, 1758
Subclass Pterygota BRAUER, 1885
Superorder Ephemeroidea LATREILLE, 1810
(= Panephemeroptera CRAMPTON, 1928)

Family Triassoephemeridae SINITSHENKOVA & PAPIER
n. fam.

Type genus: *Triassoephemera* SINITSHENKOVA & PAPIER n. gen.

Diagnosis: Nymph. Mayflies of middle size with thick cuticle, body not flattened and abdomen lacking side protrusions. Prothorax wide. Metathorax well developed but shorter than mesothorax; wing pads very short. Legs of normal length, tarsi with hairs and double claw. Gills present on first seven abdominal segments, appearing as small rounded plates densely fringed on the borders. Cerci segmented and paracercus shorter and more slender.

Comparison: The nymphs of Triassoephemeridae n. fam. differ from those of all the known living and fossil mayflies in their unflattened body, tergalia structure and double claws.

Triassoephemera SINITSHENKOVA & PAPIER n. gen.

Derivatio nominis: Generic name after the Triassic age of the specimens and the genus name *Ephemera*.

Type species: *Triassoephemera punctata* n. gen. n. sp., only represented by nymphs.

Diagnosis: As for the family.

Triassoephemera punctata SINITSHENKOVA & PAPIER
n. sp.
Figs. 2A–D

Derivatio nominis: Species name after “punctatus” (Lat.) = punctuated, which indicates the punctuated ornamentation of the nymph segments.

Holotype: 6626/6627 part and counterpart of a nymph (Figs. 2A, B), GRAUVOGEL and GALL collection.

Paratypes: 9244 (Gottenhouse, Bas-Rhin, France); 9250 (Bust, Bas-Rhin, France); 9246, 9248, 9249 (Figs. 2C, D), 9251 (Adamswiller, Bas-Rhin, France); 6628, 9243 (Arzviller, Moselle, France).

Locus typicus: Arzviller (Moselle, France).

Stratum typicum: Grès à Voltzia, Upper Buntsandstein, early Middle Triassic.

Diagnosis: As for the family.

Description: Nymph. Head rounded, middle part of prothorax slightly longer than the side parts, with a maximum length almost equal to the mesothorax length; metathorax slightly shorter than mesothorax. Fore wing pads obviously longer than the hind ones, only covering them slightly. Abdominal segments short and wide, the third one being the widest. All segments are covered with small black dots densely arranged of which the delineation forms a curious hook-shaped indentation on the fore rim of each segment (Fig. 2C). The tergaliae present on the first abdominal segments appear as small rounded plates densely fringed on the borders (6626/6627: Fig. 2 B).

Measurements: Body length of a young nymph (9246): 15 mm; of the holotype (6626/6627): 20 mm; and of a nymph at a more advanced stage (6628): 30 mm.

Remarks. The legs end in a double claw, as in the specimen 9249 (Fig. 2D) but sometimes, when the legs are in side view, the claw seems to be single, as in the mid leg of the specimen 6626/6627 (Fig. 2A).

The specimens corresponding to *Triassoephemera punctata* n. sp. represent 2.5 % of all the Ephemeroidea present in the GRAUVOGEL and GALL collection.

Order Ephemeroidea LATREILLE, 1810
(= Ephemeroptera HYATT & ARMS, 1890, sensu lato)
(= Euephemeroptera KLUGE, 2000)
Family Misthodotidae SELLARDS, 1909

Triassodotes SINITSHENKOVA & PAPIER n. gen.

Derivatio nominis: After the Triassic age and some similarity with the genus name *Misthodotes* SELLARDS, 1909.

Type species: *T. vogesiacus* n. gen. n. sp., only represented by fore and hind wings.

Diagnosis: Fore wing almost three times longer than wide, with anterior margin convex; SC not reaching wing apex; MA forking almost in its middle and having the anterior branch longer than the posterior one; MP dividing near wing base; CuA simple. Hind wing similar in shape to the fore wing except in being obviously shorter and in having a weaker and reduced venation.

Comparison: *Triassodotes* n. gen. shows similarities with *Misthodotes* but it clearly differs from it in the branching of MP near the wing base and relatively shorter hind wing.

Remarks: The costal brace characteristic of all Misthodotidae is absent in the diagnosis of *Triassodotes* n. gen., because the very base of the costal area is not preserved. MP1 and MP2 seem not to be connected basally, but usually these veins do not fuse at the acute angle. As a rule MP2 base makes a wide rounded loop before fusion; unfortunately this proper loop is not obvious on the best specimen (holotype) and on its photon.

The tendency in hind wing shortening shown by the Permian species of *Misthodotes* (TSHERNOVA 1965: 357, text-figs. 6–7; KINZELBACH & LUTZ 1984: 252, text-fig. 4) is still more pronounced in the new genus *Triassodotes*.

Until now, the family Misthodotidae was only known from the Permian of Central Europe, Germany (KINZELBACH & LUTZ 1984: 247), the Urals (TSHERNOVA 1965: 353) and Kansas, Oklahoma, USA (SELLARDS 1909: 151; CARPENTER 1979: 261). The discovery in the Grès à Voltzia of a genus belonging to this family proves that it crossed the Permian/Triassic boundary.

Triassodotes vogesiacus SINITSHENKOVA & PAPIER
n. sp.
Figs. 3A, B, 4A, B

Derivatio nominis: Species name after the Vosges Mountains (France) from where the material originates.

Holotype: 5337/5338 (Figs. 3A, 4A), part and counterpart of a fore wing with well preserved venation. GRAUVOGEL and GALL collection.

Material: Besides the holotype, there are 21 paratypes: Fore wings: 5419/5420, 5476, 5477/5478, 5938/5939, 5946, 5947/5948, 5951/5952, 5953/5954, 5955/5956, 5963/5962, 5967/5968, 5974 from Arzviller (Moselle, France); 5960; 5961 from Vilsberg (Moselle, France); 9148 from Adamswiller (Bas-

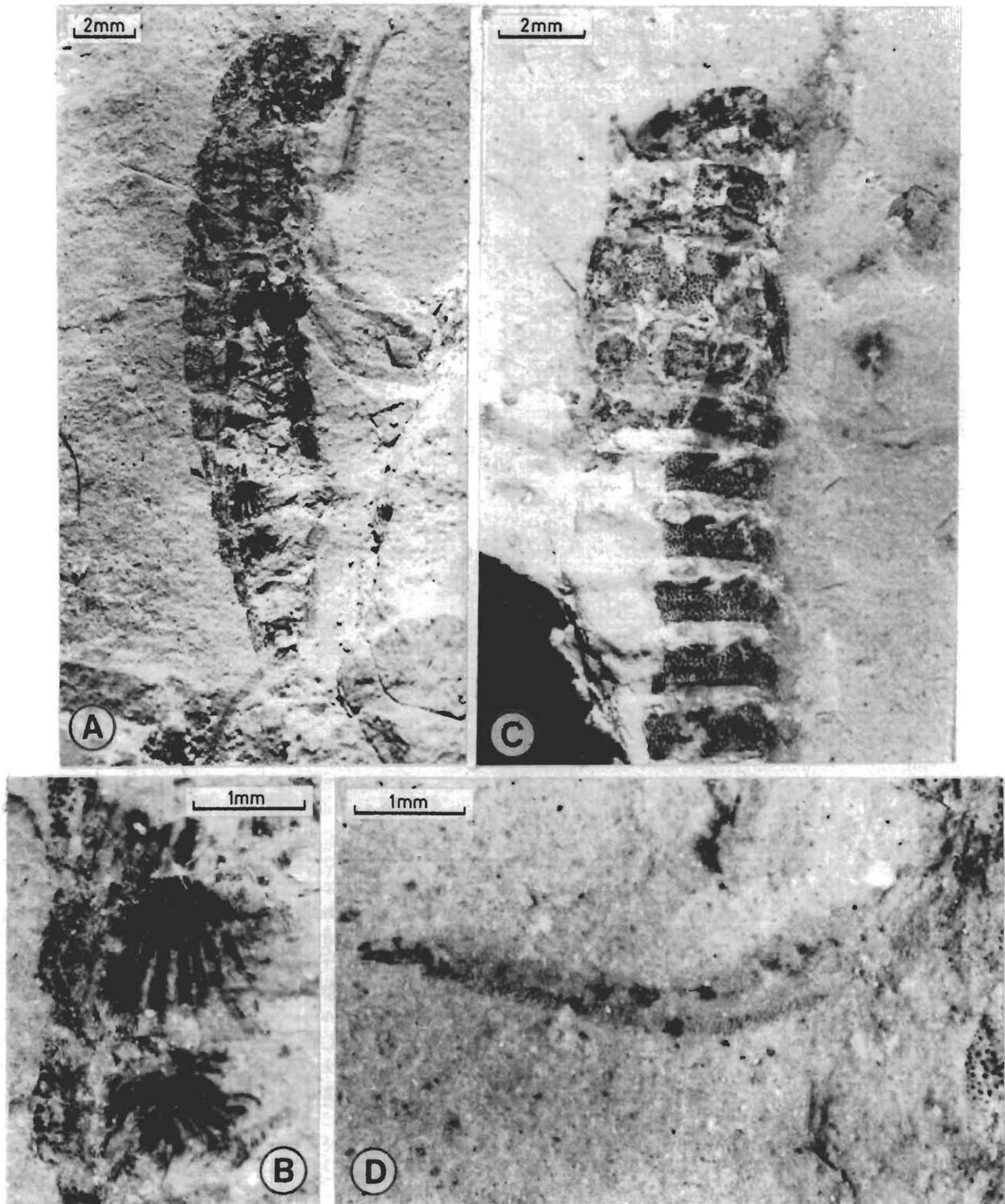


Fig. 2. *Triassoephemera punctata* n. gen. n. sp. (Triassoephemeridae n. fam.). **A, B:** holotype 6626/6627 (Arzviller, Moselle, France). **A.** nymph, **B.** tergalia. **C, D:** Paratype 9249 (Adamswiller, Bas-Rhin, France). **C.** nymph, note the segments covered with small black dots, densely arranged, **D.** hind leg with double claw.

Rhin, France). Hind wings: 5935/5936, 5937 (Figs. 3B, 4B), 5944/5945, 5971/5972, 9252, 9253 from Arzviller (Moselle, France).

Locus typicus: Arzviller (Moselle, France).

Stratum typicum: Grès à Voltzia, Upper Buntsandstein, early Middle Triassic.

Diagnosis: As for the family.

Description: In adult fore wings (Figs. 3A, 4A), SC length is 0.7 of wing length; RS reaches the wing margin with five branches and one intercalate vein; the anterior branch of MA is longer than the posterior one

which is almost straight; the branches of MP and IMP are slightly curved; CuA is also slightly curved whereas CuP is straight and ends in a short narrow fork. Hind wing (Figs. 3B, 4B) is 0.7 times as long as fore wing. Its anterior margin is somewhat rumpled at the base. SC is long and reaches the anterior margin at the apical third of wing; the subcostal area is three times wider than the costal one. R almost reaches the wing apex and RS which has five branches separates off from it near the wing base; M and Cu systems are reduced and consist of weak veins which cannot be interpreted in more details.

Measurements: Fore wing: 5.5 mm long and 1.3 mm wide; hind wing: 4 mm long and 2 mm wide.

Remarks: The specimens corresponding to the species *Triassodotes vogesiacus* n. sp. represent 6 % of all the Ephemeroidea present in the GRAUVOGEL and GALL collection.

Family Toxodotidae SINITSHENKOVA & PAPIER n. fam.

Type genus: *Toxodotes* SINITSHENKOVA & PAPIER n. gen.

Diagnosis: Small mayflies with fore wing having an arched anterior margin and a rounded apex; costalisation weakly developed, tornus not obvious, SC short, R not reaching wing apex; RS multibranching; MA and CuA almost dichotomous; MA forking in the proximal half of wing and devoid of intercalate vein, MP probably forking near the middle of wing and having a long intercalate vein. CuA with short fork.

Comparison: The Toxodotidae n. fam. resembles the Mithodotidae and Litophlebiidae in having suboval fore wings lacking distinct tornus, but it differs clearly from them by the concave anterior margin of the fore wing and by the lack of intercalate veins in MA and Cu systems. The dichotomous branching of M and CuA is a plesiomorphous feature which occurs very rarely in mayflies.

Toxodotes SINITSHENKOVA & PAPIER n. gen.

Derivatio nominis: Generic name from "toxon" (Greek) = arc, according to the arched anterior margin of the wing and after a part of the genus name *Mithodotes* SELLARDS, 1909.

Type species: *T. coloratus* n. gen. n. sp., only represented by fore wings.

Diagnosis: The same as for the family.

Toxodotes coloratus SINITSHENKOVA & PAPIER n. sp.
Figs. 3C–E, 4C, D

Derivatio nominis: Species name from "coloratus" (Lat.) = coloured, according to the patch of colour still present on the wing apices.

Holotype: 5942/5943 (Figs. 3C, D, 4C) part and counterpart of a fore wing devoid of its cubital and anal parts. GRAUVOGEL and GALL collection.

Paratype: 5949/5950 (Figs. 3E, 4D) Arzviller (Moselle, France).

Locus typicus: Arzviller (Moselle, France).

Stratum typicum: Grès à Voltzia, Upper Buntsandstein, early Middle Triassic.

Diagnosis: As for the family.

Description: In adult, SC reaches C in the apical third of wing length; costal and subcostal areas wide. RS 5-branched; the posterior branch of MA may have a short fork. M forks at the wing base whereas MA and MP branch off at almost half of their length. The wing apex is always coloured.

Measurements: Fore wing is 6.0 mm long and 1.6 mm wide in its biggest width.

The specimens corresponding to *Toxodotes coloratus* n. sp. represent 0.5 % of all the Ephemeroidea present in the GRAUVOGEL and GALL collection.

Family Voltziaephemeridae SINITSHENKOVA & PAPIER n. fam.

Type genus: *Voltziaephemera* SINITSHENKOVA & PAPIER n. gen.

Diagnosis: Nymph. Head with hairs and large lateral eyes having a protruding anterior margin and a pair of well-developed convergent tusks forward directed which have a simple inner edge, without denticles. Legs of burrowing type, i.e., well developed, covered with many hairs and ending in a terminal single claw. Wing pads long and narrow, anterior pads not covering the posterior ones. Tergalae on the first seven segments being laterally fringed with numerous long slender filaments. Small black-coloured coma-shaped sclerified structures present on the lateral parts of each segment. Paracercus well developed but distinctly more slender and shorter than the cerci.

Comparison: The Voltziaephemeridae n. fam. clearly differs from the modern ones containing burrowing nymphs in having long and narrow wing pads.

Remarks: The Voltziaephemeridae n. fam. cannot be classified in the Ephemeroidea, since the Recent ephemeroideans have heteronomous wings with Cu and M curved at the base. Judging from the wing pads of the fossil nymphs of Voltziaephemeridae n. fam., the adults should have wings devoid of an obvious tornus. As to the tusks projecting out from the anterior margin of the head, it is impossible to determine from where exactly they originate. By analogy with Recent burrowing mayfly nymphs, they might be mandibular tusks of the

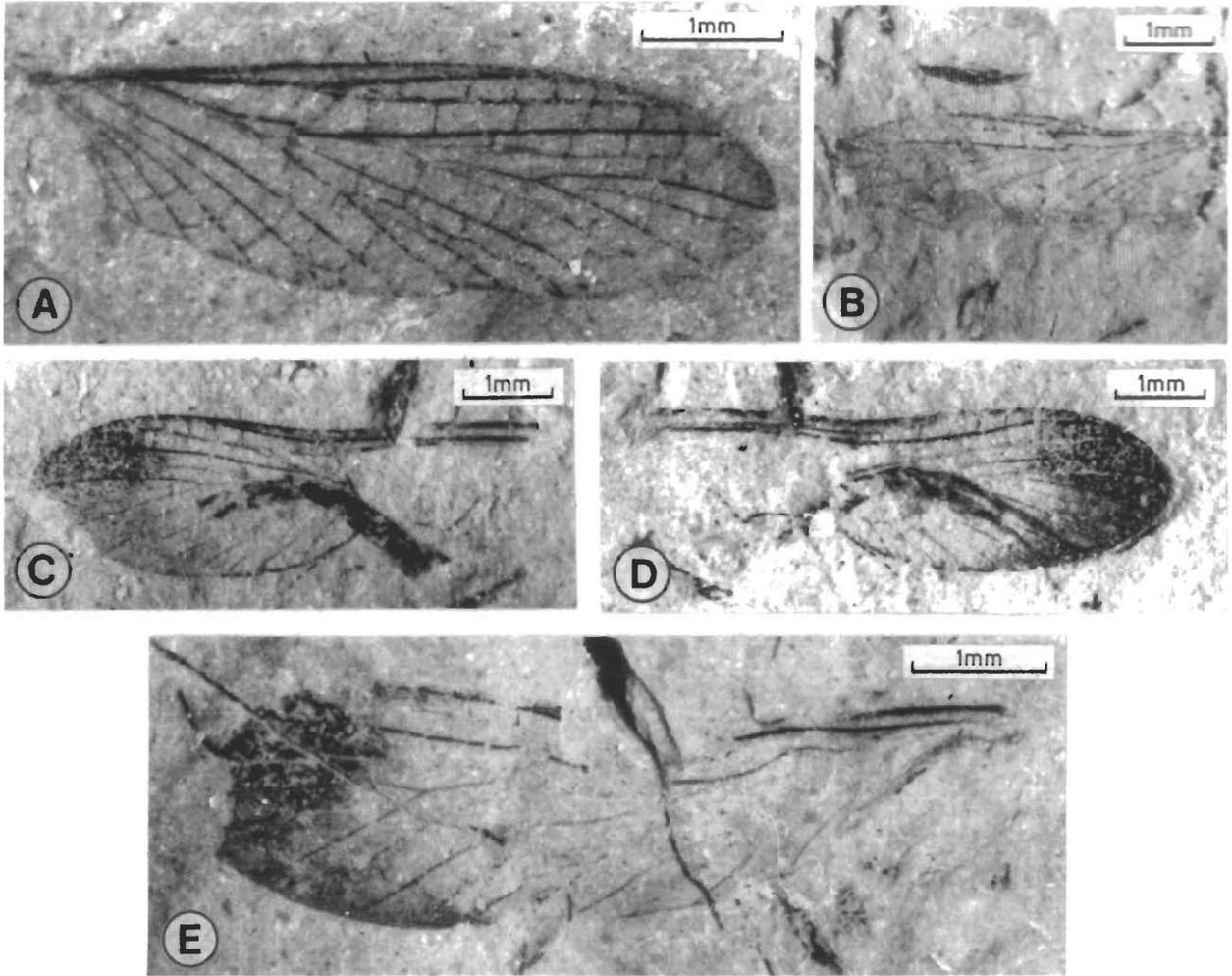
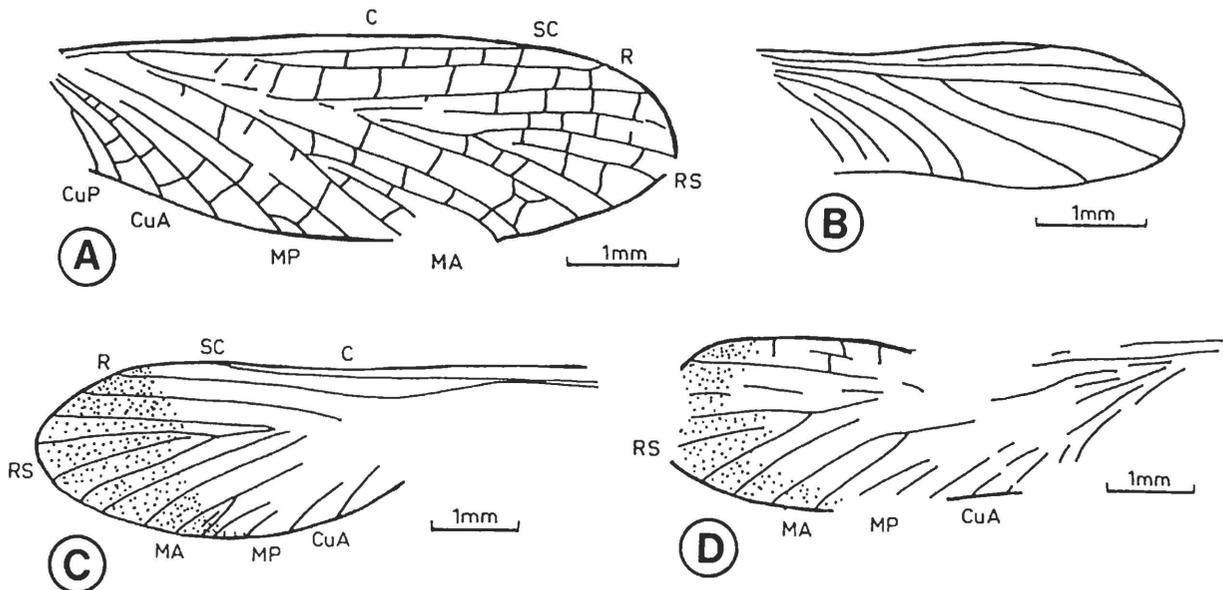


Fig. 3. – **A, B:** *Triassodotes vogesiacus* n. gen. n. sp. (Misthodotidae). **A.** forewing, holotype 5337/5338, **B.** hind wing, paratype 5937 (Arzviller, Moselle, France). – **C–E:** *Toxodotes coloratus* n. gen. n. sp. (Toxodotidae n. fam.). **C, D.** part and counterpart of a forewing, holotype 5942/5943, **E.** forewing, paratype 5949/5950. (Arzviller, Moselle, France).

Fig. 4. – **A, B:** *Triassodotes vogesiacus* n. gen. n. sp. **A.** interpretative drawing of the fore wing shown in Fig. 3A, **B.** interpretative drawing of the hind wing shown in Fig. 3B. – **C, D:** *Toxodotes coloratus* n. gen. n. sp. **C.** interpretative drawing of the fore wing shown in Fig. 3C, **D.** interpretative drawing of the fore wing shown in Fig. 3E.



Ephemera type (BAE & MCCAFFERTY 1995: 394, text-fig. 12).

Voltziaephemera SINITSHENKOVA & PAPIER n. gen.

Derivatio nominis: Genus name after the geological formation Grès à Voltzia and after the genus name *Ephemera*.

Type species: *Voltziaephemera fossoria* n. gen. n. sp., only represented by nymphs.

Diagnosis: Nymph. Head with rounded protrusion on the anterior margin. Tusks slightly projecting out from the anterior head margin. Fore legs shorter than hind legs; tibiae lacking sharp protrusion.

Voltziaephemera fossoria SINITSHENKOVA & PAPIER
n. sp.
Figs. 5A–E, 6A–F

Derivatio nominis: Species name from “fossio” (Lat.) = burrow.

Holotype: 6622/6623 represented by an entire nymph (Figs. 5A, 6C), GRAUVOGEL and GALL collection.

Paratypes: 9220 from Bust (Bas-Rhin, France); 9163 (Figs. 5B, 6F), 9217 (Fig. 5C), 9218 from Adamswiller (Bas-Rhin, France); 9111 (Fig. 5E), 9221, 9229 (Fig. 6A, B, E) from Arzviller (Moselle, France); 6621 (Fig. 5D), 9238 (Fig. 6D) from Vilsberg (Moselle, France) and about 240 samples from different localities.

Locus typicus: Adamswiller (Bas-Rhin, France).

Stratum typicum: Grès Voltzia, Upper Buntsandstein, early Middle Triassic.

Diagnosis: As for the family.

Description: Nymph. Head with hairs (9229) almost twice as wide as long, with a protrusion (especially well visible in the paratype 9111: Fig. 5E) on its anterior broadly rounded margin and close to it, the tusks which are almost joined and situated in the middle. Prothorax almost rectangular, longer than the head. Fore leg about a third of body length; hind leg 0.4 times of the body length. Cerci more than twice shorter than the body length.

Measurements: The nymph body is 14–20 mm long.

Remarks: *V. fossoria* n. sp. is the most abundant mayfly species in the Triassic of the Vosges mountains constituting more than 63.5 % of the total number of mayfly remains present in the GRAUVOGEL and GALL collection. However, a lot of specimens are macerated and therefore poorly preserved. The features of *V. fossoria* n. sp. (head with a hump, tusks forwards prolonged, both tibia and femora widened and covered with numerous hairs, gills inserted on the back) show clearly that these larvae are of the burrowing type and were adapted to an underground way of life. The numerous U-shaped trace fossils (Fig. 5F) present in the Grès à Voltzia were probably made by these larvae.

Family Triassomanthidae SINITSHENKOVA & PAPIER
n. fam.

Type genus: *Triassomanthus* SINITSHENKOVA & PAPIER n. gen.

Diagnosis: Nymph. Head short with big eyes and an anterior margin devoid of any protrusion; tusks sharp and projecting forwards out from the anterior margin. Legs comparatively long and slender, not of burrowing type; tarsi 4-segmented ending in a single claw. Metathorax clearly visible; wing pads long, oval and narrow; fore wing pads not completely covering the hind legs. Seven pairs of single tergaliae lacking fringes. Paracercus weakly developed, very slender and considerably shorter than cerci.

Comparison: This family differs from the others in having nymphs with 4-segmented tarsi, long tusks, long and narrow wing pads, seven pairs of tergaliae and non burrowing legs. The combination of long tusks and non burrowing legs occurs in the recent Potamanthidae, but according to other features, the Triassomanthidae are not related to this family.

Triassomanthus SINITSHENKOVA & PAPIER n. gen.

Derivatio nominis: Generic name after the Triassic age and part of the Ephemera genus name *Potamanthus* PICTET.

Type species: *Triassomanthus parvulus* SINITSHENKOVA & PAPIER n. gen. n. sp., represented only by nymphs.

Diagnosis: The same as for the family.

Triassomanthus parvulus SINITSHENKOVA & PAPIER
n. sp.
Figs. 7A–E

Derivatio nominis: Species name from “parvulus” (Lat.) = small, indicating the small size of the nymphs in this species.

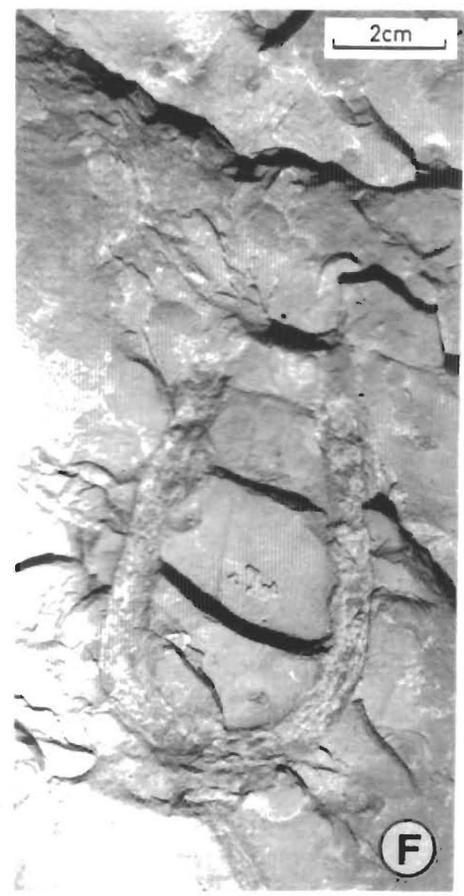
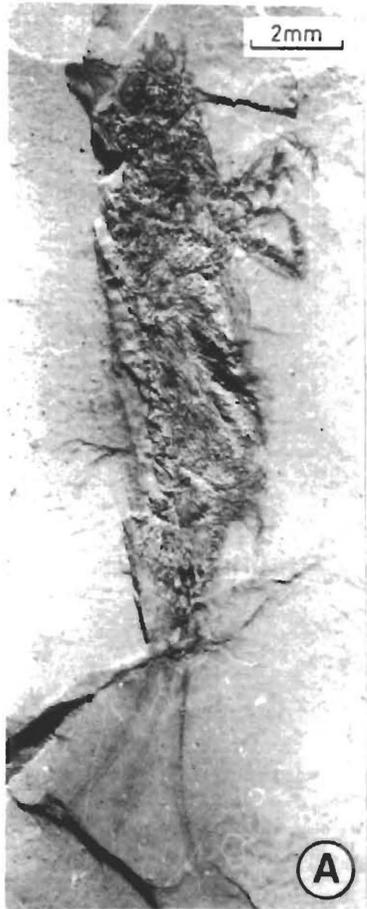
Holotype: 9153 represented by an entire nymph (Fig. 7A), GRAUVOGEL and GALL collection.

Paratypes: 6620 (Fig. 7C), 9340 (Fig. 7E) 9235, 9314, 9316, 9317, 9318, 9323, 9324, 9329, 9330, 9338, 9339 from Vilsberg (Moselle, France); 9159 (Fig. 7D), 9337 (Fig. 7B) 9315, 9320, 9331, 9333, 9334, 9335, 9336 from Arzviller (Moselle, France); 9307, 9312, 9313, 9319; 9321, 9322, 9325, 9327, 9332 from Bust (Bas-Rhin, France); 9254, 9326 from Adamswiller (Bas-Rhin, France); 9328 from Schoenbourg (Bas-Rhin, France).

Locus typicus: Bust (Bas-Rhin, France).

Stratum typicum: Grès à Voltzia, Upper Buntsandstein, early middle Triassic.

Fig. 5. *Voltziaephemera fossoria* n. gen. n. sp. (*Voltziaephemeridae* n. fam.), nymphs. **A:** holotype 6622/6623. **B:** paratype 9163. **C:** paratype 9217 (Adamswiller, Bas-Rhin, France). **D:** paratype 6621, (Vilsberg, Moselle, France). **E:** paratype 9111 (Arzviller, Moselle, France). **F:** U-shaped gallery 9342 (Vilsberg, Moselle, France).



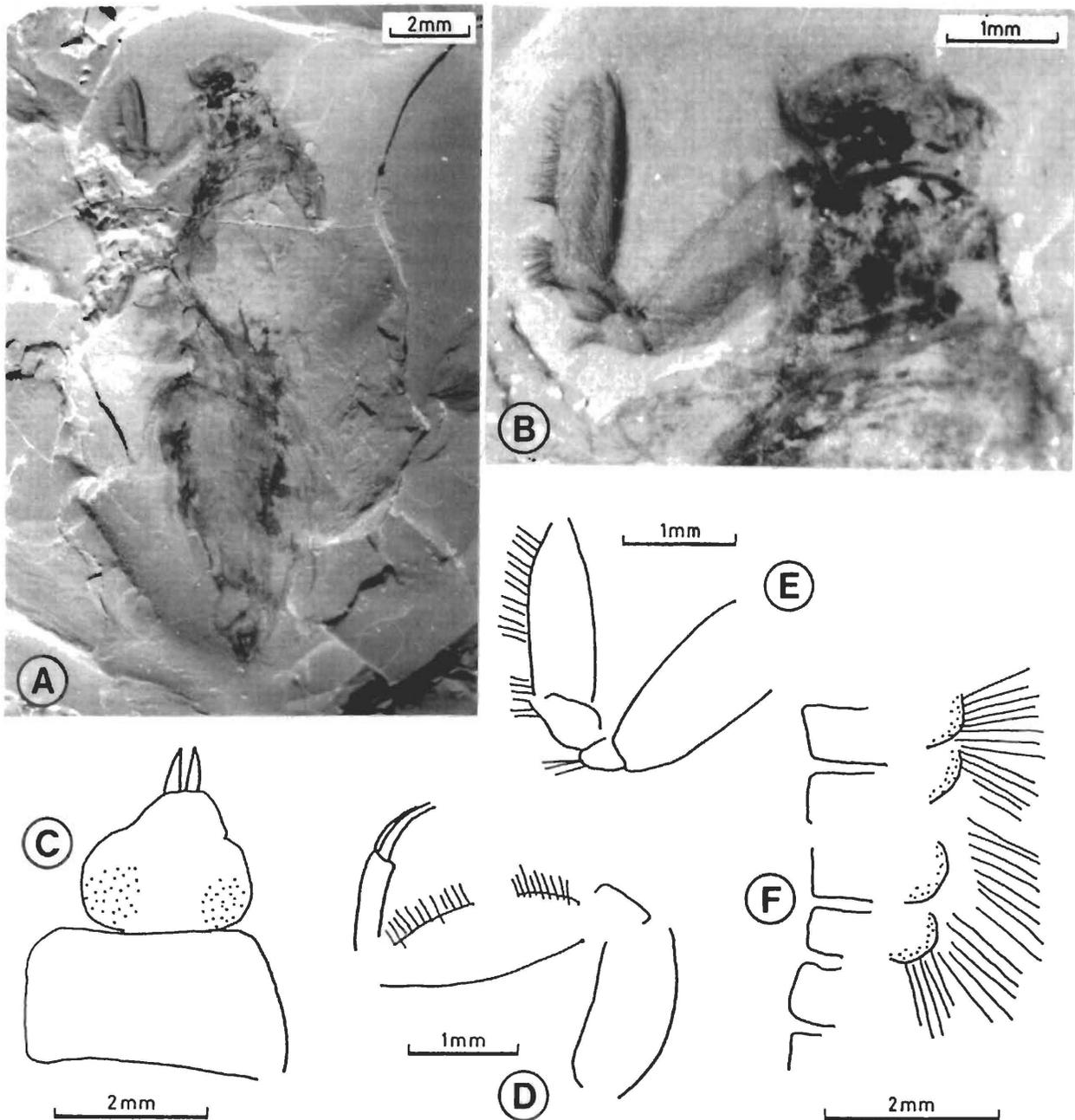


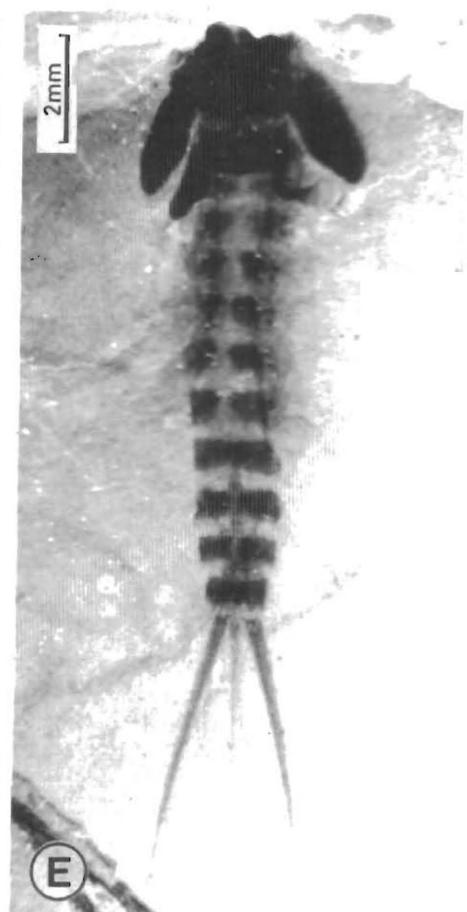
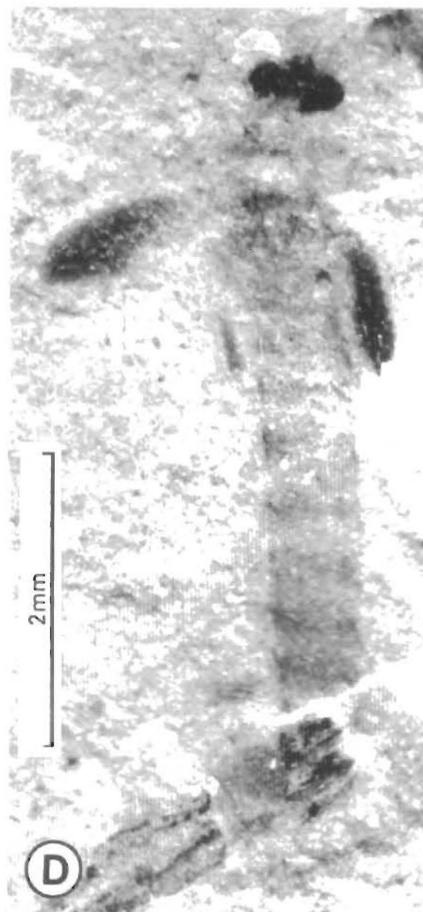
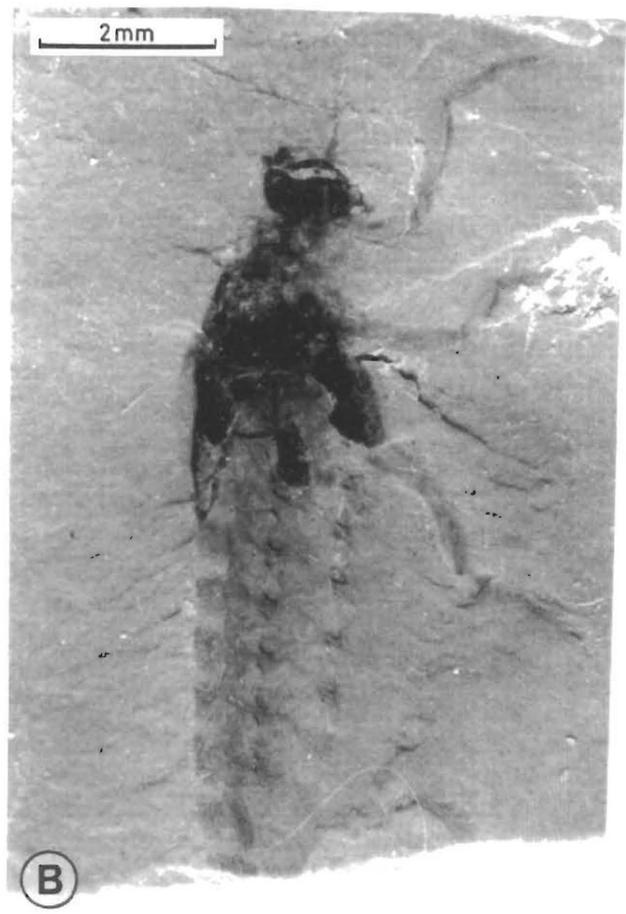
Fig. 6. *Voltziaephemera fossoria* n. gen. n. sp. (Voltziaephemeridae n. fam.). **A, B:** paratype 9229 (Arzviller, Moselle, France). **A:** nymph, **B:** detail of its head, thorax and fore leg. **C:** interpretative drawing of the head and prothorax of the nymph shown in Fig. 5A. **D:** interpretative drawing of a fore leg (paratype 9238, Vilsberg, Moselle, France). **E:** interpretative drawing of the fore leg shown in Fig. 6B. **F:** interpretative drawing of an abdomen portion with tergalia shown by the nymph in Fig. 5B.

Diagnosis: As for the family.

Description: Nymph. Head 1.5 wider than long and shorter than prothorax; antennae almost twice as long as the head (6620, Fig. 7C); protruding part of tusks almost as long as head (6620); big lateral eyes (6620). Protho-

rax about twice as wide as long, having a slightly concave anterior margin and convex posterior margin, with widely rounded hind angles and sharp fore angles. Mesothorax rectangular, higher than wide and heart-shaped with the tip forwards directed. Fore femora almost as long as tarsi and 0.6 times as long as tibiae; claw single,

Fig. 7. *Triassomanthus parvulus* n. gen. n.sp. (Triassomanthidae fam. nov.), nymphs. **A:** holotype 9153 (Bust, Bas-Rhin, France). **B:** paratype 9337 (Arzviller, Moselle, France). **C:** paratype 6620 (Vilsberg, Moselle, France). **D:** paratype 9159 (Arzviller, Moselle, France). **E:** paratype 9340 (Vilsberg, Moselle, France).



3 times shorter than tarsus (visible in the paratype 9337); fore legs with hairs (visible in the paratype 9339). Abdominal segments short and wide. Tergalae very thin, oval in shape and narrowing towards the apex, with weak margins and black coma-shaped structures. Paracercus 3 times shorter than cerci.

Measurements: Body length 6.2–10.6 mm.

Remarks: The paracercus is so slender that it is often hardly visible in the fossil remains. The specimens corresponding to the species *Triassomanthus parvulus* n. sp. represent 9 % of all the Ephemeroidea present in the GRAUVOGEL and GALL collection.

Family Mesopteropteridae DEMOULIN, 1955

Diagnosis: Nymph. Mayflies of middle size. Head and prothorax small; metathorax well developed; wing pads long and narrow, backwards and laterally directed; hind pads protruding out of fore pads. Legs with very long and slender femora and tibiae. Cerci long, widely separated.

Comparison: The Mesopteropteridae differs from all the other families in having very long and slender legs. Neither Recent mayflies nor fossil ones have comparable long legs. TSHERNOVA (1980: 32) assigned to the Mesopteropteridae an adult with very long legs from the Permian of Germany which was previously figured by VÖLKE (1959: 395, text-figs. 6–7).

Mesopteropterum HANDLIRSCH, 1918

Type species: *M. longipes* HANDLIRSCH, 1918.

Diagnosis: As for the family.

Mesopteropterum longipes HANDLIRSCH, 1918 Figs. 8A–D

*1918 *Mesopteropterum longipes* HANDLIRSCH: 113.

Holotype: HANDLIRSCH'S original specimens (shown here in Figs. 8A, B) housed in the EOST-Géologie, Université Louis Pasteur, Strasbourg.

Material: Besides the holotype, three further specimens corresponding to this species are present in the collection GRAUVOGEL and GALL: nymphs 9200 (Fig. 8D) from Arzviller (Moselle, France); 9199 (Fig. 8C), 9201 from Adamswiller (Bas-Rhin, France).

Description: Nymph. Head short with rounded anterior margin and wide posterior margin. Prothorax shorter than head, rectangular, with slightly rounded angles. Fore wing pads reaching second abdominal segment. Fore legs almost as long as body. Abdominal segments short, 2–2.5 times wider than long. Cerci longer than half of body.

Measurements: The body is 9–9.7 mm long.

Remarks: The long antennae figured by HANDLIRSCH (1918: 113) are not visible in the holotype which is poorly preserved. The specimens corresponding to the species *Mesopteropterum longipes* represent 1 % of all the Ephemeroidea present in the GRAUVOGEL and GALL collection.

Family Siphonuridae ULMER, 1920 (s.l.)

Triassonurus SINITSHENKOVA & PAPIER n. gen.

Derivatio nominis: Generic name combining the Triassic age and part of the type-genus name *Siphonurus* EATON.

Type species: *Triassonurus doliiformis* n. sp., only represented by nymphs.

Diagnosis: Large nymph with a non flattened body. Head obviously longer than the prothorax which is short. Mesothorax massive and metathorax considerably shorter; fore wing pads large and wide, almost completely covering the hind ones. Legs short and slender. Abdominal segments without sharp denticles at posterior angles. Tergalae very large, rounded, with thickened anterior margin. Cerci and paracercus long.

Comparison: *Triassonurus* n. gen. differs from the other genera of the family in having a large mesothorax and large rounded tergalae.

Remarks: The Siphonuridae is known from the Jurassic until the Holocene. Therefore, *Triassonurus* n. gen. is the most ancient representative of the family.

Triassonurus doliiformis SINITSHENKOVA & PAPIER n. sp. Figs. 9A–C

Derivatio nominis: Species name from “doliiformis” (Lat.) = barrel-shaped, such as the shape of the abdomen.

Holotype: 9304 represented by an incomplete nymph (Fig. 9A), GRAUVOGEL and GALL collection.

Paratypes: 9280 (Fig. 9B), 9290 (Fig. 9C), 5130, 9247, 9255, 9256, 9257, 9258, 9259, 9261, 9262, 9263, 9264, 9265, 9267, 9270, 9271, 9272, 9273, 9274, 9275, 9276, 9279, 9284, 9285, 9286, 9287, 9291, 9292, 9294, 9297, 9298, 9299, 9301, 9302, 9303 from Arzviller (Moselle, France); 9281, 9293, 9296 from Vilsberg (Moselle, France); 9171 from Gottenhouse (Bas-Rhin, France); 9283 from Lutzelbourg (Moselle, France) and 9260, 9269, 9277, 9278, 9282, 9288, 9295, 9305 from Bust (Bas-Rhin, France).

Locus typicus: Arzviller (Moselle, France).

Stratum typicum: Grès à Voltzia, Upper Buntsandstein, early Middle Triassic.

Diagnosis: As for the genus.

Description: Nymph. Head triangular, wider than long and narrowing towards the anterior margin. Prothorax rectangular, four times wider than long. Fore wing pads reaching anterior margin of second abdominal segment. Femora obviously shorter than tibiae and tarsi slightly shorter than the latter. Leg seems to be single. Abdomi-

nal segments short, 2.5 times wider than long. Tergaliae overlapping each other and forming a continuous surface; the width of tergaliae is about half as broad and nearly as long as the corresponding segments; however they are longer than the corresponding segments. Cerci segmented, coloured and covered with small hairs.

Measurements of the holotype 9304 which is incompletely preserved (10 mm long) and which is supposed to have a total length of about 12 mm.

Remarks: The younger nymphs have cerci as long as the body (9296). The remains of *Triassonurus doli-*

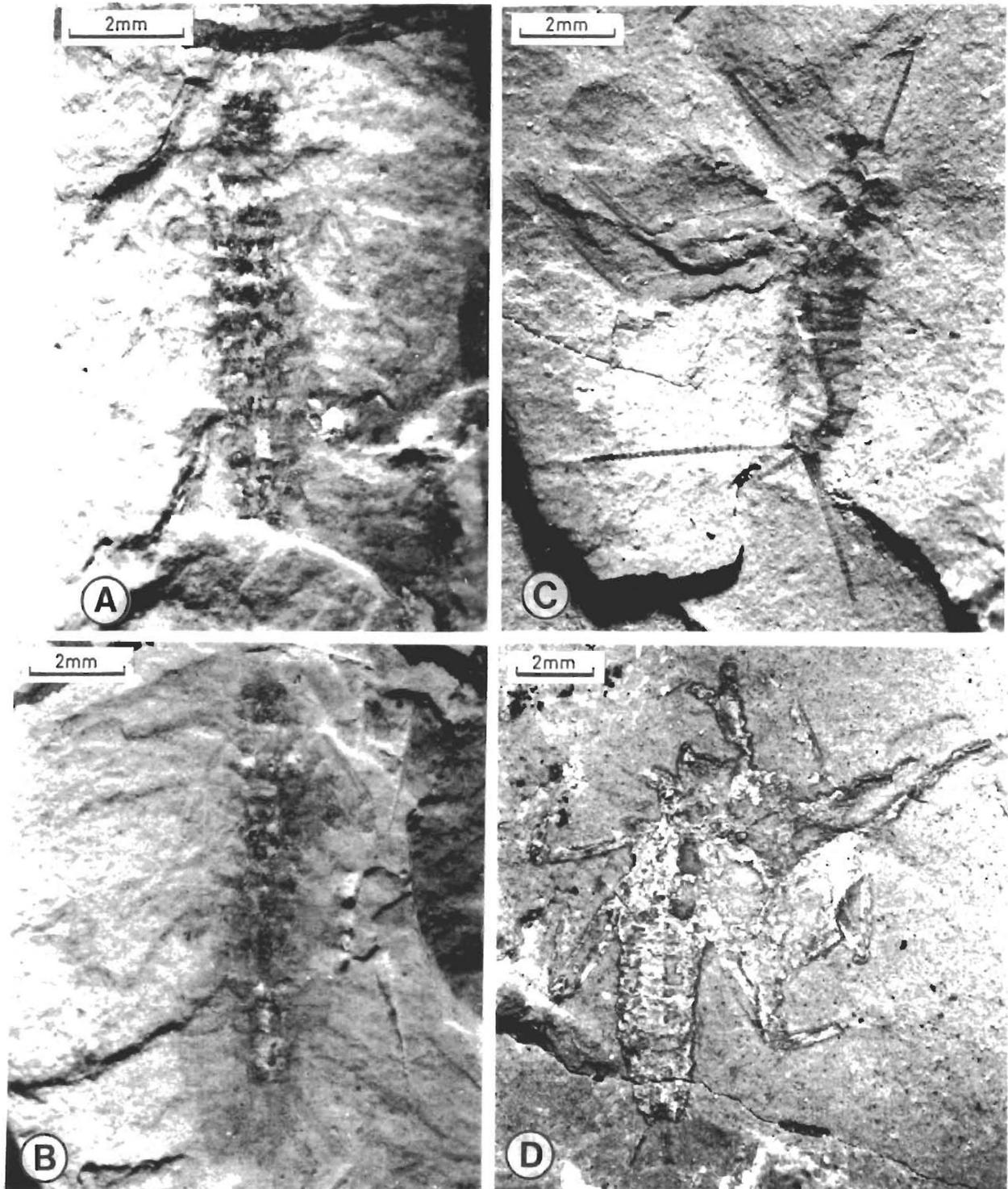


Fig. 8. *Mesoplectopteron longipes* HANDLIRSCH (Mesoplectopteridae), nymphs. **A, B:** holotype (Sultz les Bains, Bas-Rhin, France), collection HANDLIRSCH. **C, D:** collection GRAUVOGEL and GALL. **C.** specimen 9199 (Adamswiller, Bas-Rhin, France), **D.** specimen 9200 (Arzviller, Moselle, France).

formis n. sp. are very often preserved in lateral view so that the gills can be seen only on one side of the body. Such type of burial is likely due to the barrel-like shape abdomen. The specimens corresponding to *T. doliiformis* n. sp. represent 13 % of all the Ephemeroidea present in the GRAUVOGEL and GALL collection.

Family undetermined

Minorella SINITSHENKOVA & PAPIER n. gen.

Derivatio nominis: Generic name after "minor" (Lat) = small.

Type species: *Minorella virgata* n. gen. n. sp. only represented by nymphs.

Diagnosis: Nymph. Small slender mayflies with long cerci and paracercus. Head rounded, prothorax short. Legs long and slender. Seven pairs of narrow oval tergellae with thickened anterior margin.

Remarks: *Minorella* n. gen. resembles the Recent mayfly nymphs of the Leptophlebiidae (BANKS 1900), but there are not enough features to assert this attribution or to substantiate the affiliation of *Minorella* n. gen. to any other known family.

Minorella virgata SINITSHENKOVA & PAPIER n. sp.
Figs. 10A–C

Derivatio nominis: Species name from "virgatus" (Lat.) = striped, as the cerci show alternating clear and dark articles.

Holotype: 9203 represents an entire nymph (Figs. 10B, C); GRAUVOGEL and GALL collection.

Paratypes: 9202; 9204 (Fig. 10A) from Adamswiller (Bas-Rhin, France); 9205 from Arzviller (Moselle, France); 9206 from Hangviller (Moselle, France); 9207, 9212 from Bust (Bas-Rhin, France).

Locus typicus: Vilsberg (Moselle, France).

Stratum typicum: Grès à Voltzia, Upper Buntsandstein, early Middle Triassic.

Description: Nymph. Abdominal segments short; tergellae 1.5 times longer than the segments. Cerci and paracercus equal in length and about as long as body, with alternating light and dark joints (especially well visible in 9206, 9207, 9212).

Measurements of the holotype (9203): the body is 3.8–4.0 mm long; the cerci and paracercus are 3.8 mm long.

The specimens corresponding to *Minorella virgata* n. sp. represent 2 % of all the Ephemeroidea from the GRAUVOGEL and GALL collection.

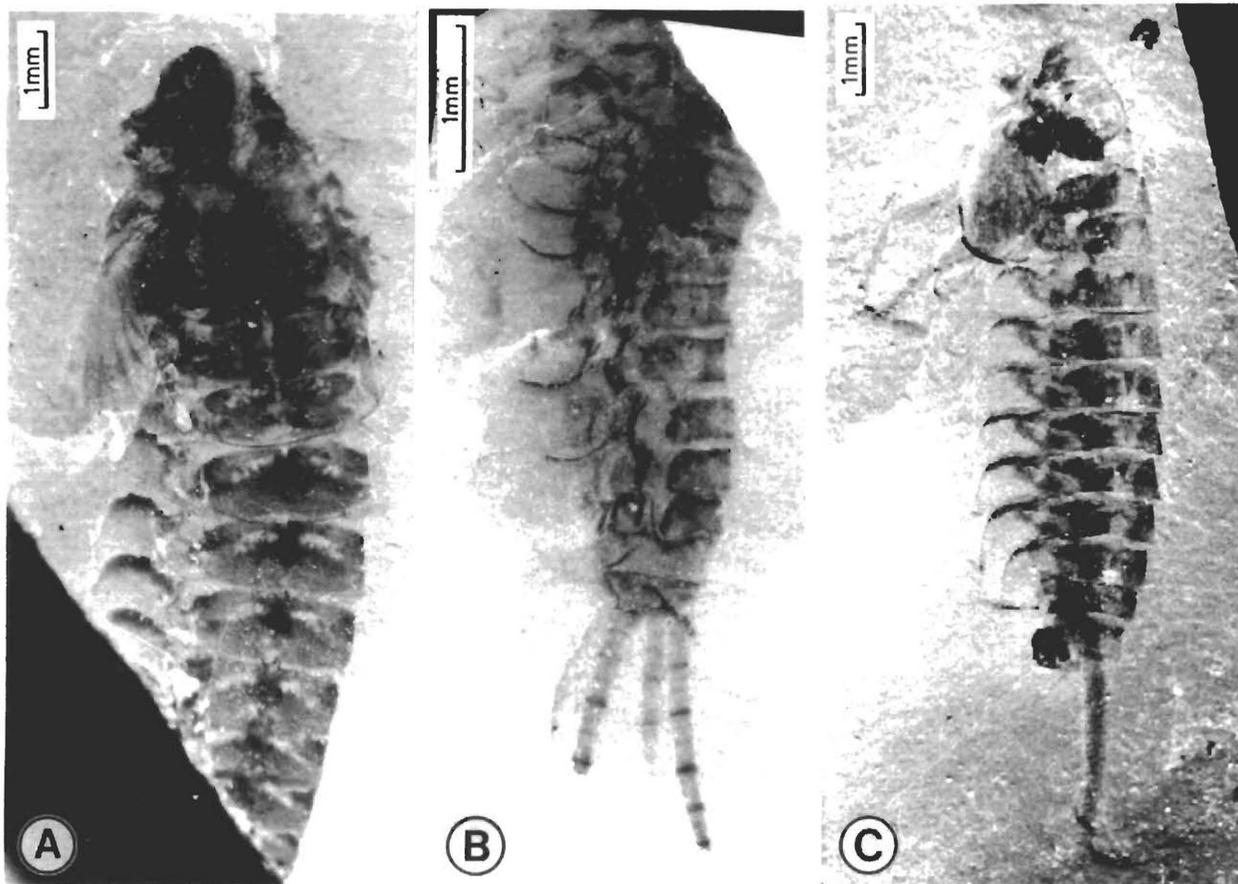


Fig. 9. *Triassonurus doliiformis* n. gen. n. sp. (Siphonuridae), nymphs. **A:** holotype 9304. **B:** paratype 9280. **C:** paratype 9290. (Arzviller, Moselle, France).

Pterygota incertae sedis

Family Vogesonymphidae SINITSHENKOVA & PAPIER
n. fam.

Type genus: *Vogesonympha* SINITSHENKOVA & PAPIER n. gen.

Diagnosis: Nymph. Body flattened, with unusually thick cuticle; prothorax large; wing pads well developed in middle and late instars; metathorax well developed but shorter than mesothorax; legs short; 4-segmented tarsi ending in a terminal pair of claws; first seven abdominal tergites with large pointed lateral protrusions; cerci long, segmented, paracercus shorter and more slender than cerci.

Comparison: The nymphs of this new family differs from the others in having large pointed lateral protrusions on the I–VII abdominal segments and 4-segmented tarsi ending in a terminal pair of claws.

Remarks: According to RASNITSYN (2002: 71, fig. 61), the fossil from the Grès à Voltzia attributed to *Vogesonympha ludovici* n. gen. n. sp. in the present work is an “enigmatic fossil” showing some similarities with *Carbotriplura* (KLUGE 1996: 72), now related to the silverfishes, but originally described as a gigantic mayfly nymph *Bojophlebia* (KUKALOVA-PECK 1985: 936, text-figs. 4–10). However, the similarity of their general appearance is superficial. Indeed, the lateral protrusions on the abdomen of both fossils are very similar but the main

difference lies in the absence of such protrusions on the segments VIII–X in *Vogesonympha* while in *Bojophlebia* such structures also occur on the last segments. The belonging of *Vogesonympha* to the mayflies seems to be confirmed by the presence of long wing pads, long segmented-cerci and long paracercus. On the contrary, the fact that Bojo is devoid of wing pads could indicate that it is either a wingless insect or a very young nymph. However the latter hypothesis seems to be wrong because of the great body length of Bojo (102 mm), suggesting that the eggs of this species must be very large, which is difficult to believe.

Vogesonympha SINITSHENKOVA & PAPIER n. gen.

Derivatio nominis: Genus name after the Vosges mountains from where the material originates and from “nympha” which, in Greek, is the term for the late instar larvae of the hemimetabolous insects.

Type species: *Vogesonympha ludovici* n. gen. n. sp., only represented by nymphs and larvae.

Diagnosis: As for the family.

Vogesonympha ludovici SINITSHENKOVA & PAPIER
n. sp.

Figs. 11A–F

Derivatio nominis: Species name after the first name of Louis GRAUVOGEL who collected the material.

Holotype: 8036 (Fig. 11A), part and counterpart of a late instar nymph, GRAUVOGEL and GALL collection.

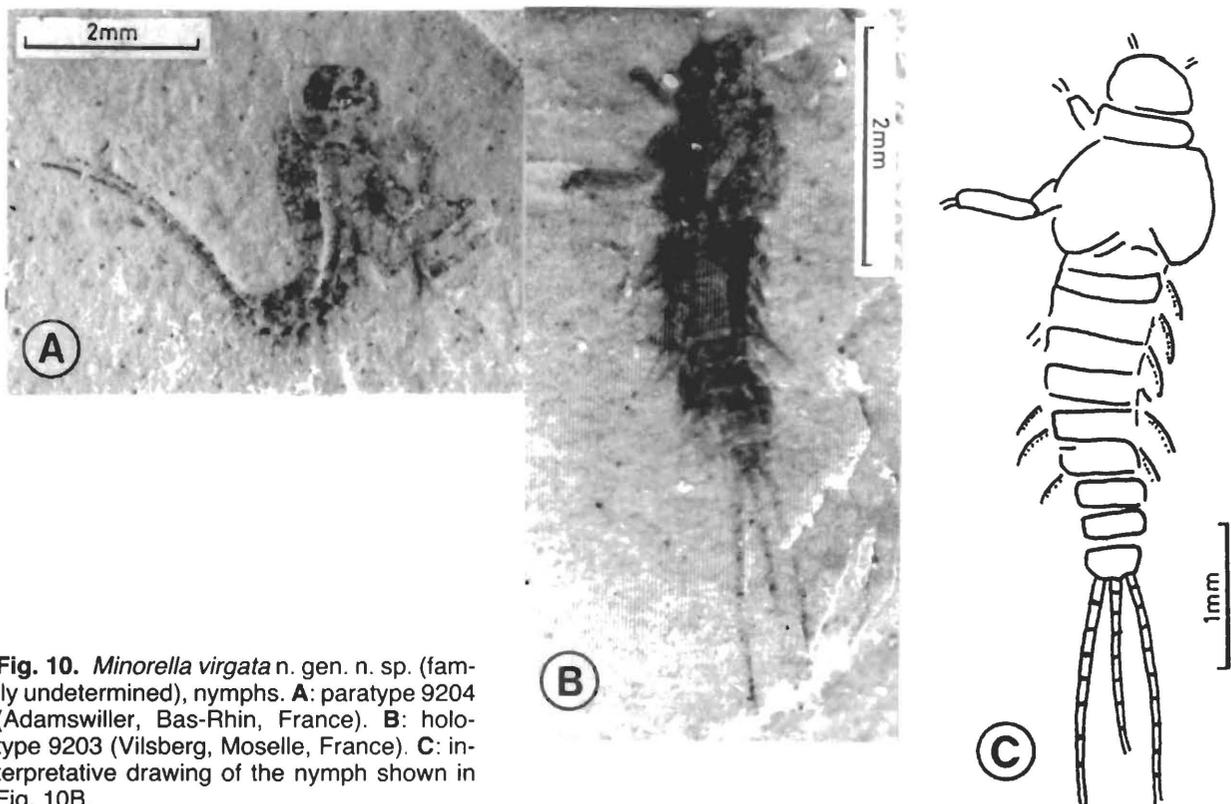


Fig. 10. *Minorella virgata* n. gen. n. sp. (family undetermined), nymphs. **A:** paratype 9204 (Adamswiller, Bas-Rhin, France). **B:** holotype 9203 (Vilsberg, Moselle, France). **C:** interpretative drawing of the nymph shown in Fig. 10B.

Paratypes: 9110, 9166 (Fig. 11B), 9208 (Fig. 11C), 9213 from Adamswiller (Bas-Rhin, France); 9209 (Figs. 11D–F), 9210, 9214, 9216 from Arzviller (Moselle, France); 9211 from Cocheren (Moselle, France); 9215 from Bust (Bas-Rhin, France).

Locus typicus: Adamswiller (Bas-Rhin, France).

Stratum typicum: Grès à Voltzia, Upper Buntsandstein, early Middle Triassic.

Diagnosis: As for the family.

Description: Nymph. Head rounded with big eyes (9210), slightly shorter than prothorax, with straight posterior margin. Prothorax 1.5 times wider than long, with anterior acute angles and posterior obtuse ones. Mesothorax slightly longer than prothorax and about twice longer than metathorax. Wing pads very short in young nymphs (specimen 9208: body length 10 mm, Fig. 11C), longer and broadly rounded at apex in middle instars (specimen 9209: body length about 12 mm, Fig. 11D), long and narrowed at apex in late instars (holotype, specimen 8036: body length about 18 mm, Fig. 11A). Legs slender and moderately long, all approximately the same length and ending in two claws (9110; 9209: Figs. 11E, F; 9210). Both femora and tibiae rather stout, subcylindrical in shape. Fore leg femora not longer than prothorax, tibiae longer than femur. Mid and hind leg tibiae shorter than corresponding femora, tarsi 4-segmented and slightly longer than tibiae; first tarsal segment seeming to be the shortest whereas the second one is the longest, the third and fourth ones being equal in length (9110). Hairs are visible on the tarsal segments along their posterior border (9110). Abdominal segments, transversely elongated and gradually narrowing towards the abdomen extremity. The first seven segments having lateral strongly developed protrusions, slightly backwards arched with pointed tips. Cerci 1.5 times shorter than abdomen and paracercus 1.5 times shorter than cerci (specimen 9166: Fig. 11B).

In the *Vogesonympa* adults, the wings must be moderately heteronomous. This is inferred from the difference in development of the metathorax and mesothorax. Indeed, the fact that the mesothorax is more developed than the metathorax suggests that the fore wings were longer than the hind wings.

Measurements: Body length of the holotype (8036) of which the last segment is missing, must reach about 18 mm; cerci length (paratype 9166): 7.5 mm; paracercus length: 4.8 mm. Body length of the paratypes 9110 and 9211 are respectively 15 mm and 10 mm.

Vogesonympa ludovici n. sp. represents 2.5 % of the Ephemeroidea present in the GRAUVOGEL and GALL collection.

Phylogeny

A number of diverse mayflies appeared in the Triassic, some of which have primitive features whereas others show advanced ones. It seems to be the time of broad radiation of mayflies. Some of these mayfly groups became extinct while the others survived until now.

The described mayfly fauna has proved interesting because of the presence of a number of ancient species related to the Protereismatidae. However, they are more advanced than the Permian representatives, which are characterized by homonomous wings. The Triassic mayflies have to some extent reduced hind wings. It is reasonable to expect that the evolution of mayfly flying organs developed from the homonomous wings towards the heteronomous ones up to the complete disappearance of hind wings. The wing shape changed considerably as well during that process; both the fore wings and the nymph fore wing pads became triangular.

Triassodotes is obviously advanced in comparison with the Permian members of the family Mithodotidae in having a greater extent of the hind wing reduction, at the same time a plesiomorphic feature of venation (namely, the basal branching of MP), probably remained from the ancestor. This character can be found not only in the Triplosobidae, a sister group to all other mayflies combined with the dragonflies, but also in living Ephemeroidea.

The Toxodotidae possess such an apomorphic feature within the suborder Protereismatina as the concave fore margin of the fore wing which is characteristic of living mayflies. However, the Toxodotidae cannot be considered to be the ancestor of them, the concavity of the fore margin could arise independently in different groups. Its oval wing shape is a plesiomorphic feature and that is the main reason against the close relation of these Triassic mayflies with the living ones.

The nymphs in the described fauna have proved to be more taxonomically diverse but their phylogenetic relations remains unclear, as the preimaginal stages of mayfly development are less known than the imaginal ones.

Vogesonympa appears to be *Pterygota incertae sedis* though it has some features (absence of paranota, presence of long wing pads, well developed long cerci and paracercus) related to mayflies. Even a jointed tarsus, double claws and wide protrusions on the abdominal segments would not exclude it from mayflies. 5-jointed tarsus and double claws are known for the older mayfly nymph *Kukalova americana* DEMOULIN (Protereismatidae) from the Early Permian of the Wellington Formation in Oklahoma (USA) (KUKALOVA 1968: 313, text-figs. 1–2; DEMOULIN 1970: 6). The abdominal protrusions often occur in different recent mayfly nymphs. Moreover one could propose that the abdominal protrusions of the first seven segments in *Vogesonympa* might protect the delicate gills.

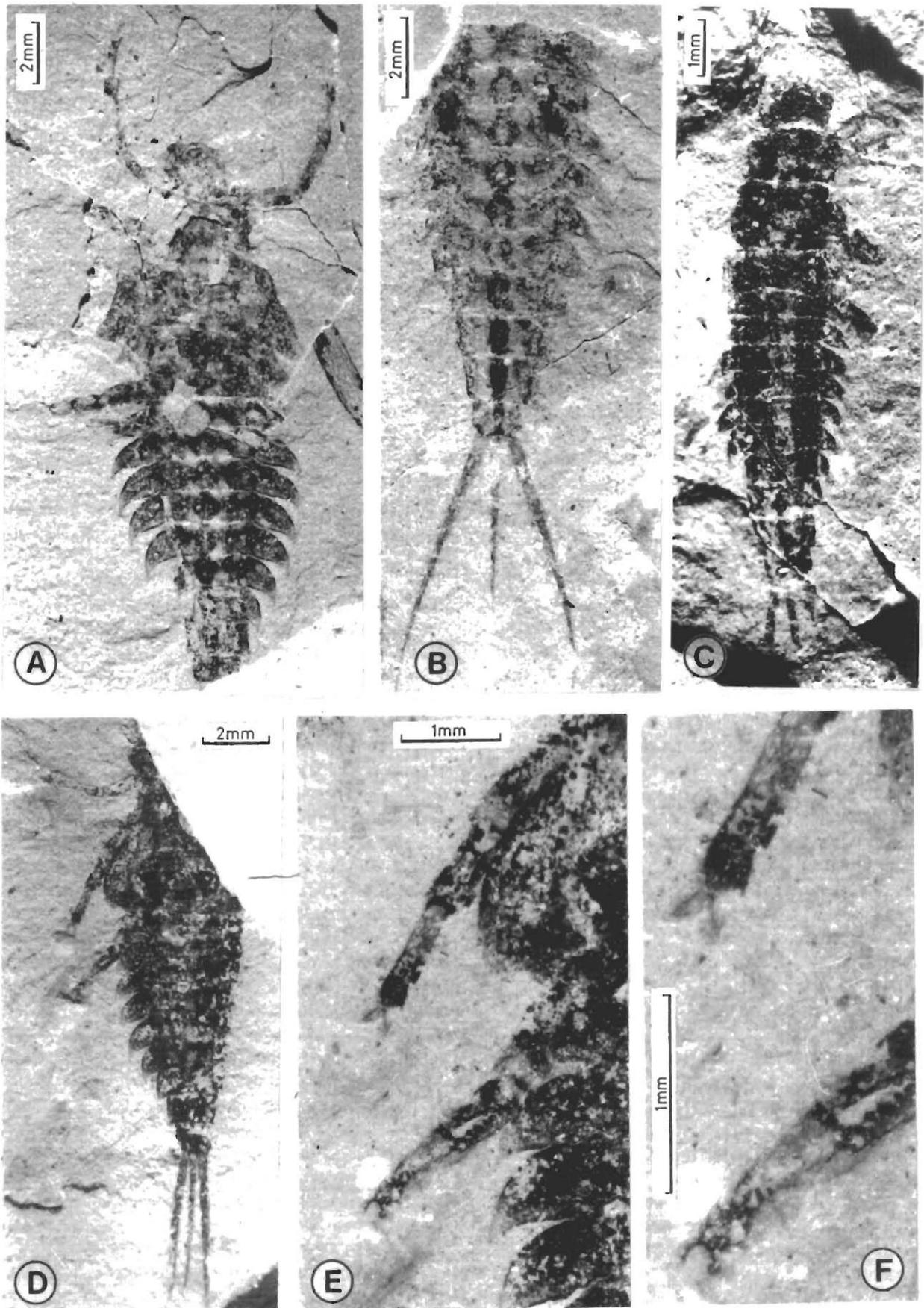


Fig. 11. *Vogesonympha ludovici* n. gen. n. sp. (Vogesonymphidae n. fam.), nymphs. **A:** holotype 8036. **B:** paratype 9166. **C:** paratype 9208. (Adamswiller, Bas-Rhin, France). **D–F:** paratype 9209 (Arzviller, Moselle, France). **D:** general view of the nymph, **E, F:** detail of its tarsi and terminal pair of claws.

The relationship of *Triassoephemera* with the true mayflies is disputable. Its thick cuticle (as well as in *Vogesonympha*) is obviously a plesiomorphy lacking in all true mayflies, the autapomorphy of which is the development of tergalia, the laminated tracheal gills on abdomen sides. The gills of *Triassoephemera* seem not to be homologous to the tergalia of mayflies. They look like small rounded plates with a densely fringed border. It should be noted that they have the general resemblance of the gills of *Siphgondwanus occidentalis* McCafferty from the Lower Cretaceous Crato Formation in Brazil. According to the drawing (McCafferty 1990: 28, fig. 9) the gills in *Siphgondwanus* look like the real tergalia, namely a large plate with short spinelike bristles. The relationship of *Siphgondwanus*, a representative of the Siphonuridae, with *Triassoephemera* is completely excluded. Another interpretation of the triassoephemerid gills is also possible. The gills might represent a bundle of gill filaments fused at the base, or looking so on the fossils. Such bundles of gills represent protrusions of thin cuticle parts and can appear in different groups of aquatic insects, as well as additional structures in mayfly nymphs inhabiting the peculiar environments. If the gills of the Triassoephemeridae are not a specific structure it should be referred to the superorder Ephemeridea incertae order. This superorder contains three orders, Triplosobida, Syntonoptera and Ephemerida (or true mayflies). For the first two orders the nymphs are unknown. This is why it is reasonable to establish a separate family Triassoephemeridae and impossible to classify it more exactly.

The similarity of the Volziaephemeridae with the living burrowing mayflies is restricted by long tusks, legs of burrowing type and densely fringed tergalia turned towards the dorsal part of the abdomen. Such characters do not mean a close phylogenetic relationship of the Volziaephemeridae with the Recent Ephemerodea. The structure of wing pads of the Volziaephemeridae demonstrates the flying apparatus of adults similar to that of the Prottereismatidae. The resemblance of the Triassic nymphs with living ones is probably due to a similar mode of life. The same can be said about *Triassomanthis*. The burrowing habit could arise in different and phylogenetically distant groups. There are similar examples in living mayflies, when the representatives of different families (Heptageniidae in the northern hemisphere and Leptophlebiidae in the southern hemisphere) inhabiting similar environments in a rapid current have a similar appearance up to forming a sticking disc by the enlarged tergalia.

The presence of long legs both in nymphs and adults of Mesopteroptera has defined the isolated position of this family similar to other Prottereismatina by oval homonomous wings.

Together with the ancient species, some forms appeared, such as *Triassonurus* and *Minorella*, that are closely related to living mayflies. *Triassonurus* is referred to the Siphonuridae (s.l.), phylogenetic relation-

ships of which are well studied in recent representatives. The definition of the fossils in this system is difficult, as many features have not been preserved or it is impossible to observe them. The similarity of *Triassonurus* with other Mesozoic siphonurids indicates most probably a similar mode of life rather than close phylogenetic relations. We could not define closer affinities of *Minorella* because of the deficiency of necessary data.

Discussion

The large number of Ephemeridea (385 specimens) in the Grès à Voltzia, their occurrence mostly as larvae and nymphs (93.5 %) and their state of preservation led us to wonder what were their habitats and life conditions like. The comparison with the living Ephemerida was very useful and instructive for determining them.

Judging from the living nymphs which are all aquatic and lived exclusively in freshwater (indeed, very few species tolerate brackish water with a salt concentration not over 3 ‰) (Illies 1968: 19; Bauernfeind 2003: 108, 116), it can be assumed that the fossil ones lived similarly and breathed dissolved oxygen. As noted earlier (Rousseau 1921: 162–272; Bertrand 1954: 215–266), the living Ephemerida nymphs are also very sensitive to oxygen concentration and water turbidity. Thus any kind of detrimental change to these life conditions make them die.

The great number of Ephemeridea larvae present in the Grès à Voltzia proves that the lakes and ponds where they lived contained, at least temporarily, limpid and well-oxygenated freshwater. Moreover, the fact that many larvae reach the nymph stage indicates that these conditions must last long enough to allow their development. Judging from the living Ephemerida and depending on the species, the complete larval development can span a period of some months to three years (Rousseau 1921; Bertrand 1954). However, the fact that a great number of larvae are found fossilized together on a small surface of the silty-clayey lenses of the Grès à Voltzia suggests that a severe change in environmental conditions occurred, resulting in their mass mortality. This is particularly clear in the case of the species *Voltziaephemera fossoria* n. gen. n. sp. of which a great number of nymphs are fossilized close to one another. The turbidity and salinity increase resulting from evaporation and/or from salty water supply was probably the reason of their mass mortality. Indeed, salinity variations have clearly been noted in the Grès à Voltzia (Gall 1971: 175).

None of the nymphs have their mouth parts well enough preserved to establish their feeding habits with certainty; most of them were probably debris collectors or algal feeders except for burrowing nymphs which could have been filter feeding.

Among the different types of Ephemerida nymphs present in the Grès à Voltzia, some of them are similar to living ones. According to their morphological fea-

tures and adaptations to different habitats, the living Ephemeroidea nymphs are classified in four (ROUSSEAU 1921; BERTRAND 1954) or twelve types and subtypes (TSHERNOVA 1952: 294).

The burrowing larvae are characterized by rather short and stout legs, by gills turned up towards the back, by the development of protuberances in front of the head and by the presence of huge, forward directed tusks. All these morphological features are tools for burrowing. They are shown by the species *Voltziaephemera fossoria* n. gen. n. sp. from the Grès à Voltzia. The way of life of these fossil Ephemeroidea was probably similar to that of the living burrowing mayfly nymphs which make U-shaped galleries mostly in the banks of large rivers. Indeed, the lot of finely scratched U-shaped trace fossils present in the Grès à Voltzia suggest that, at least, part of them have been made by the nymphs of *Voltziaephemera fossoria* n. gen. n. sp. which was the most abundant Ephemeroidea in the Grès à Voltzia. One of these specimens shows an U-shaped gallery measuring 40 mm long, of which the two branches are 10 mm distant and 4 mm in diameter (Fig. 5F). The fact that these galleries are of different size suggests the occurrence of Ephemeroidea nymphs at different stages and sizes. As the living burrowing Ephemeroidea, the fossil ones must live in quiet water where they could find the requisite conditions for burrowing. By moving their tergalia and owing to the openings present at both extremities of the U-shaped galleries, they must make the water flow and then collect the food particles. Likewise, they must have had to leave the galleries and burrow new ones when they grew bigger or when the water level changed. The U-shaped galleries of the Grès à Voltzia have already been interpreted as the holes of some invertebrates, crustaceans or Ephemeroidea (GALL 1971: 69, 1976: 51).

As to the nymphs of *Triassonurus doliiformis* n. gen. n. sp., they resemble living nymphs with large tergalia which inhabited the near shore places, in large rivers with slow current. These nymphs which live among water plants, can swim quickly away when they are disturbed. On the contrary, the Ephemeroidea larvae which live in brooks with weak current have narrow tergalia and long cerci. They must crawl on the bottom among plant remains. The nymphs of *Minorella* can be referred to this morpho-ecological type.

However, it is impossible to find any ecological equivalent among the living mayflies for the nymphs of *Vogesonympha*, *Triassoephemera*, and *Mesoptopteron*. Indeed, the very thick cuticle shown by *Vogesonympha* and *Triassoephemera* is not typical for mayfly nymphs. It is likely that this feature was retained from ancestors which probably lived near the water level, in wet shore environments which were periodically flooded. Such a habitat cannot be excluded for *Vogesonympha* and *Triassoephemera*. The small tergalia with dense fringe observed in *Triassoephemera punctata* n. gen. n. sp. probably served for maintaining a certain humidity rather than for breathing. This type of nymph

may represent some extinct high-level taxa unknown from younger strata. The very long and slender legs in *Mesoptopteron* are unique among the mayflies and required to create a new family. Although this nymph has widely stretched cerci which can also be observed in rheophilous mayflies, it represents an enigmatic species among the Ephemeroidea. The Mesoptopteroidea nymphs probably lived in rivers, occupying the places where the current was weak and water plants occurred. Their long legs must help them to remain in place and to prevent them from being swept away by the current.

According to the morphology of all the mayfly nymphs studied in this work, we can assume that they lived in the quiet zones of the ponds and lakes which were strewn over the deltaic environment that existed during the deposition of the Grès à Voltzia.

Besides the Ephemeroidea larvae, a lot of other animals, such as fishes, crustaceans, and other aquatic insect larvae (Megaloptera, Plecoptera) inhabited the lakes of the Grès à Voltzia. The Ephemeroidea larvae were surely a prey for this fauna and constituted an important part of the food for the fishes and crustaceans.

Conclusions

As the present study shows, the Ephemeroidea were well represented and very diversified in the early Middle Triassic. Moreover, like the other insect orders from the Grès à Voltzia of the Vosges (of northeastern France), they include archaic representatives inherited from the Paleozoic, some original forms and still others already announcing modern lineages. The wing named *Triassodotes vogesiacus* n. gen. n. sp. which is classified in the family Misthodotidae is close to the Paleozoic Ephemeroidea. It shows that this Permian family crossed the Permo-Triassic boundary, and may suggest that the biotic crisis which occurred at that time was not as destructive, at least concerning the insects, as generally admitted. On the contrary, as to the nymph *Vogesonympha ludovici* n. gen. n. sp., it shows original and strange features which are unknown in any other fossil and/or living Ephemeroidea. Likewise, *Triassoephemera punctata* n. gen. n. sp. is an enigmatic nymph. As to *Mesoptopteron longipes* HANDLIRSCH, it is characterized by long and slender legs which are also unknown in fossil and Recent Ephemeroidea. On the contrary *Triassonurus doliiformis* n. gen. n. sp. is a nymph which belongs to a modern lineage. Indeed, it resembles the nymphs of the Siphonuridae and therefore it has been classified in this family which is also known since the Jurassic. *Voltziaephemera fossoria* n. gen. n. sp. which is a burrowing mayfly, is the most abundant form (63.5 %) in the Grès à Voltzia. Its ecology is comparable to that of the modern burrowing species. The abundance and diversity of Ephemeroidea nymphs in the Grès à Voltzia indicates that they found favourable conditions to their development. Judging from the living Ephemeroidea nymphs, it can be assumed that the water of the ponds and lakes

where they lived and which were strewn over the paleo-delta of the Grès à Voltzia, was at least temporarily, limpid and well-oxygenated freshwater.

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