The oldest occurrence of immature Diptera (Insecta), Middle Triassic, France

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Abstract. The oldest fossil Diptera are known from the Grès à Voltzia Formation (Upper Buntsandstein) of the northern Vosges Mountains (northeastern France), the age of which is early Anisian (early Middle Triassic). Six monotypic genera assigned to all the major lineages of Diptera (except for the Culicomorpha) were described from these beds based on adults (Krzeminski *et al.* 1994; Krzeminski & Krzeminska 2003). Immature Diptera also occur in the Grès à Voltzia (ca 30 specimens). Pupae are abundant whereas the larvae are extremely rare. The most numerous and well-preserved pupal type has been assigned to *Voltziapupa* **n. gen.** (*V. tentata* **n. sp.** and *V. cornuta* **n. sp.**). These pupae display plesiomorphic characters combined with possibly derived ones. Among the larvae, *Anisinodus crinitus* **n. gen., n. sp.** shows culicomorph features. It represents the earliest Culicomorpha (Chironomoidea *inc. fam.*) known up to date. The other types of dipteran immatures (six pupal and two larval ones) occurring in the Grès à Voltzia are less well preserved, so that their systematic position is difficult to determine and they have been assigned to the Nematocera *incertae sedis*. These immature Diptera are the first ones recorded from the Triassic.

Résumé. La plus ancienne occurence de diptères immatures (Insecta), Triassique Moyen, France. Le plus ancien fossile de diptère est connu de la formation des Grès à Voltzia (Buntsandstein supérieur) du nord des Vosges (nord-est France), dont l'âge correspond à l'Anisien ancien (Triassique Moyen ancien). Six genre monotypiques assignés a toutes les grands groupes de diptères (sauf les culicomorphes) ont été décrits de ces dépôts sous leur seule forme adulte (Krzeminski *et al.* 1994; Krzeminski & Krzeminska 2003). Des diptères immatures existent aussi dans les Grès à Voltzia (ca 30 spécimens). Les pupes sont abondantes tandis que les larves sont extrèmement rares. Les pupes les plus nombreuses et les mieux préservées ont été attribuées à *Voltziapupa* **n. gen.** (*V. tentata* **n. sp.** et *V. cornuta* **n. sp.**). Ces pupes présentent des caractères plésiomorphes combinés avec d'autres possiblement dérivés. Parmi les larves, *Anisinodus crinitus* **n. gen.**, **n. sp.** présente des caractéristiques culicomorphes, ce qui représente le plus ancien culicomorphe connu à ce jour (Chironomoidea *inc. fam.*). Les autres diptères immatures des Grès à Voltzia (six pupes et deux larves) sont moins bien préservés de telle sorte que leur position systématique est difficile à déterminer ce qui mène à les considérer comme des nématocères *incertae sedis*. Ces diptères immatures sont les premiers connus du Triassique.

Keywords: Diptera, immatures, pupae, larvae, Chironomoidea, oldest record.

In the middle of the twentieth century Louis Grauvogel (1947a, b) announced the discovery of several thousand insects in the Grès à Voltzia (Upper Buntsandstein) of the northern Vosges Mountains (northeastern France), the age of which was demonstrated to be early Anisian (Gall 1971: 184). Among these insects Grauvogel found and labelled several dozens of Diptera. More recently, Marchal-Papier (1998) reported that Diptera were abundant in the Grès à Voltzia (an uncommon situation for the Triassic) and estimated their number at about 280 specimens, or 5.3% of total number of collected insects (more than half of them, 59%, were larvae assigned without description to "species 3" by Marchal-Papier 1998). The first dipteran described from these beds was *Grauvogelia arzvilleriana* Krzeminski, Krzeminska & Papier 1994, based on numerous well-preserved isolated wings: they constitute more than half of the 70 collected adult Diptera (Krzeminski *et al.* 1994). Later on, Krzeminski & Krzeminska (2003) described further five species (four of them in new genera) each based on a single adult specimen: *Louisa nova* Krzeminski & Krzeminska 2003 (Grauvogeliidae), *Tanus triassicus* Krzeminski & Krzeminska 2003 (Nadipteridae), *Archilimonia vogesiana* Krzem-

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inski & Krzeminska 2003 (Archilimoniidae), *Vym-rhyphus blagoderovi* Krzeminski & Krzeminska 2003 (Protorhyphidae), and *Gallia alsatica* Krzeminski & Krzeminska 2003 (Rhagionidae).

These Diptera are the most ancient described members of the order known to date. The supposed Diptera were recorded from the nearly synchronous Buntsandstein (Anisian) of Mallorca, but they are undescribed vet (Calafat Colom 1988; Zessin 2008). The other Triassic Diptera have been described from the Carnian of Australia (Kovalev 1983a; Blagoderov 1999; Lukashevich & Shcherbakov 1999) and North America (Krzeminski 1992; Blagoderov et al. 2007), the Ladinian/Carnian and Norian/Rhaetian of Asia (Shcherbakov et al. 1995), the Rhaetian of Europe (Krzeminski & Jarzembowski 1999; Krzeminski & Krzeminska 2002), and also recorded from the Carnian of Africa (Anderson & Anderson 1993). However, in spite of intensive research, immature stages of Diptera have never been found in the Triassic. In contrast, in his first paper on the fauna of the Grès à Voltzia of the Vosges, Grauvogel (1947a) already noted that dipteran pupae probably occurred among his finds. Recently Marchal-Papier (1998) and Krzeminski and Krzeminska (2003) similarly noted the presence of immature Diptera in the Grès à Voltzia without describing them. The present paper deals with these fossils. We describe the first dipteran immatures from the Triassic. Although their systematic position cannot be determined accurately, they are worth to be described.

Material and methods

Triassic insects are known from 13 localities in the northern Vosges Mountains (for details of the geographic situation, see Sinitshenkova et al. 2005). We have re-examined those determined as Diptera in the collection and have noted that they occur in four localities: Arzviller and Vilsberg in the Moselle department, Adamswiller and Bust in the Bas-Rhin department, both in the northeastern France. Most of the Diptera specimens, about one hundred, come from Arzviller (some 80 of them, including all the wings of Grauvogelia, are from the same lens), and only a very small part comes from the three other localities. Among the immature specimens, the pupae are more numerous (about thirty specimens, mostly exuviae) and more diverse than the larvae. They have been collected from the four localities, but also mostly from Arzviller, and in almost all the lenses containing adult Diptera. In contrast, only three undoubted dipteran larvae have been found in three localities, whereas many supposed ones actually belong to other orders (most of them are poorly preserved mayfly nymphs), indicating that previously the number of Diptera in the assemblages was about twice overestimated.

All the fossils under description are housed in at the private collection of Louis Grauvogel, Strasbourg, France. The numbering of the specimens in the collection is somewhat heterogeneous. Indeed, the specimens including a counterpart are indicated by either a number followed by the sign " \pm " or by two successive numbers separated by an oblique line. The small letter which sometimes follows the number means that it is one of the several impressions occurring on the same slab.

The photographs were made using Leica MZ9.5 stereomicroscope with Leica DFC420 digital camera, with further correction using Adobe Photoshop CS 9.0 software.

The infraordinal concept is after Hennig (1968, 1973), who divided the nematocerous Diptera into four infraorders: Tipulomorpha, Psychodomorpha, Culicomorpha and Bibionomorpha (for reasons, see Lukashevich & Shcherbakov 1999). The system is after Shcherbakov *et al.* (1995).

Taxonomy

Order Diptera

Family ?Grauvogeliidae Krzeminski, Krzeminska & Papier 1994

Genus Voltziapupa n. gen.

Type species. Voltziapupa tentata n. sp.

Other species. *Voltziapupa cornuta* **n. sp.** from the Middle Triassic of France described below.

Diagnosis. Pupa dark, subcylindrical. Head with a pair of more or less developed frontal horns (fh). Mesothoracic respiratory horn (rh) cylindrical, very elongate, with a slight apical widening. Antennae (an) lying back over ocular areas, consisting of no less than 14 moniliform segments. Dorsum of cephalothorax smooth, without large setae. Wing sheaths (ws) reaching mid-length of body (segment IV of abdomen). Split of exuviae (mc) running along midline from well-developed metanotum (mtn) to the head. All leg sheaths (ls) directed backwards, lying subparallel to each other, side by side, not covering each other and ending approximately level with the apex of wing sheaths, mid and hind leg sheaths partially under wing sheaths; leg sheaths unequal in length, fore legs shortest, ending before wing sheath apices, and hind leg longest, distal parts of mid and hind tarsi curved medially. Abdominal tergite I somewhat wider than the metanotum; all abdominal segments subequal, tergites more sclerotized than sternites, abdominal segments without secondary segmentation, with one row of small, sparse spines along posterior margin.

Etymology. The genus is named after Grès à Voltzia Formation and the pupal stage of development. Gender feminine.

Remarks. There are several reasons to assign these abundant and well-preserved pupae to *Grauvogelia arzvilleriana* described previously based on wings (for details, see Discussion). However the venation of the wing sheath, which is partly visible only on the holotype of *Voltziapupa tentata* **n. sp.** (Figs 1A, 2A), is not preserved well enough to verify this assignment. So a new genus should be established for these pupae.

According to our observations, it is sure that none of the leg sheaths is recurved beneath the wing sheaths, and in the pupa 5447 all the legs are doubtless parallel



Photographs of the pupae of *Voltziapupa tentata* **n. gen., n. sp.** from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). **A,** holotype at left and paratype 6592b at right (Vilsberg). **B,** paratype 9076 (Arzviller). **C,** paratype 5447 (Arzviller). **D,** paratype 9084 (Arzviller); **E–F,** part and counterpart of paratype 9105a (Arzviller); **G,** paratype 9085 (Arzviller). Scale bar = 1 mm. an – antennal sheath, ls – leg sheath, mtn – metanotum, mc – middorsal cleft, rh – respiratory horn, ws – fore wing sheath.



Line drawings of the pupae of *Voltziapupa* **n. gen.** from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). A–F, *Voltziapupa tentata* **n. sp. A**, holotype (Vilsberg) from Fig. 1A. **B**, paratype 5447 (Arzviller) from Fig. 1C. C–D, paratype 9076 (Arzviller), **C**, anterior portion on part, **D**, antenna and respiratory horn on counterpart from Fig. 1B. **E**, tip of leg and wing sheaths of paratype 9105a (Arzviller) from Fig. 1F. **F**, genital sheath on counterpart of paratype 6591b (Vilsberg), G–I, *Voltziapupa cornuta* **n. sp. G–H**, part from Fig. 7A and counterpart of paratype 9106 (Arzviller). **I**, holotype (Arzviller) from Fig. 7B. Scale bar = 1 mm, except for Figs 2D–2F enlarged (not to scale). an – antennal sheath, fh – frontal horn, lp – lateral process, ls – leg sheath, mc – middorsal cleft, mtn – metanotum, rh –respiratory horn, ws– fore wing sheath.



Figure 3

Photographs of the chaetotaxy of the Diptera pupae from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). A-B, *Voltziapupa tentata* **n. gen.**, **n. sp.: A**, holotype (Vilsberg), tergite IV. **B**, paratype 9084 (Arzviller), tergite IV. **C**, *Voltziapupa cornuta* **n. gen.**, **n. sp.:** holotype (Arzviller), tergite V. D–F, Nematocera *incertae sedis*. **D**, gen. sp.1: 9080 (Arzviller), tergite VI. **E**, gen. sp.2: 9067 (Bust), tergite IV. **F**, gen. sp.4: 9074, (Arzviller), thorax. Scale bar = 0.25 mm.

to each other (Figs 1C, 2B). However the mid and hind leg sheaths seem to be slightly superimposed in the specimens 6591a, 6591b, 9076, 9082, 9105a, 9106 (Figs 1A, 1F, 2A, 2E, 2G). Possibly it means that the leg sheaths were not glued to the body and so they can occupy different positions (especially in pliant cast skins) at their burial. The same seems to be true for the antennal sheaths (see cast skins 9076, 9085 and especially 9084, in Figs 1B, 1D, 1G, 2D). Hence these pupae probably were exarate (*i.e.* with appendages free from the body).

Voltziapupa tentata n. sp. (Figs 1, 2A–2F, 3A–3B, 4A–4B)

Diagnosis. Frontal horns small.

Holotype. Pupa 6591a/6592a (Vilsberg, Moselle) (Figs 1A, 2A).

Paratypes. Pupae 5447 (Arzviller), 6589/6590 (Adamswiller), 6591b/6592b (Vilsberg), 6593/6594 (Adamsviller), 9071 (Vilsberg), 9075± (Arzviller), 9076± (Arzviller), 9084± (Arzviller), 9085 (Arzviller), 9087± (Arzviller), 9102a±, c, d± (Arzviller), 9103 (Arzviller), 9105a±, b (Arzviller), 9107 (Arzviller).

Stratigraphy and collecting locality. Grès à Voltzia (Upper

Buntsandstein) of the northern Vosges Mountains, northeastern France.

Age. Early Anisian, *i.e.* early Middle Triassic.

Description. Pupa 4–5 mm long (exuviae 6–7.5 mm), wing sheath 1.5–2 mm long and about 1 mm wide. Frontal horns presumably small (9102c, d, 9105a, 9107); respiratory horns very long and thin, about 1 mm long, subequal to mesothorax and antennal sheath, with a distinct apical widening (Figs 1A, 1B, 2A, 2C, 2D). Row of dark spines not very dense, about 10–12 spines per 0.5 mm (Figs 3A, 3B, 4A, 4B). Abdominal segment IX with lateral processes (Fig. 2F).

Etymology. The species name refers to the systematic position of the new species that must be proven, put to the test (from Latin *tentatus*).

Remarks. The differences in length of the pupa and its cast skin result from the fact that in the exuviae the abdomen is usually extended and its segments become widely separated from one another by the intersegmental membranes. We observed this trait also in many recent Nematocera.

Voltziapupa cornuta n. sp. (Figs 2G–2I, 3C, 4C, 7A–7B)

Diagnosis. Frontal horns large. **Holotype.** Pupa 9082± (Arzviller) (Figs 2I, 7B).



Line drawings of the chaetotaxy of the Diptera pupae from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). A-B, *Voltziapupa tentata* **n. gen., n. sp.: A**, holotype (Vilsberg), tergite IV. **B**, paratype 9084 (Arzviller), tergite IV. **C**, *Voltziapupa cornuta* **n. gen., n. sp.:** holotype (Arzviller), tergite V. D–G, Nematocera *incertae sedis.* **D**, gen. sp.1: 9080 (Arzviller), tergite VI. **E**, gen. sp.2: 9067 (Bust), tergite IV. **F**–G, gen. sp.4: 9074, (Arzviller), thorax and tergite VI. Scale bar = 0.25 mm.

Paratypes. Pupae 9096 ± (Arzviller), 9106± (Arzviller).

Stratigraphy and collecting locality. Grès à Voltzia (Upper Buntsandstein) of the northern Vosges Mountains, northeastern France.

Description. Pupa *ca* 4.5 mm long without intersegmental areas and 7.5 mm with them. Wing sheath 2 mm long and about 1.5 mm wide. Frontal horns large (Figs 2G, 2I, 7A, 7B). Respiratory horns elongate, about 1mm long, not longer than mesothorax, apex not preserved. Row of dark spines not very dense, about 10 spines per 0.5 mm (Fig. 4C).

Etymology. The species name refers to the large frontal horns (from Latin *cornutus* = bearing horns).

Remarks. These pupae are very similar to those assigned to *V. tentata* **n. sp.**, except for the frontal horns which are more developed than in the type species. However the degree of development of the frontal horns may vary within a genus, as for example in the Chironomidae (*Glyptotendipes* Kieffer 1913, pers. obs.).

The wing sheaths of one specimen (9106) possess an acute tip (Figs 2G, 2H, 7A), whereas in the two other specimens (9082, 9096) they are rounded (Figs 2I, 7B). It is impossible to understand whether it is an artifact caused by the underlying leg sheaths or if it is the actual peculiarity of this wing sheath. Wing sheaths with an acute tip are known in many recent Psychodidae with pointed wings, e.g. in *Clytocerus* Eaton 1904 and *Psychoda* Latreille 1796, whereas in *Sycorax* Haliday 1839 with rounded wings the wing pads are also rounded at the apex (Brauns 1954 and pers. obs.). However, pointed wings are unknown among the adult Diptera from Vosges.

Chironomoidea incertae familiae

Genus Anisinodus n. gen.

Type species. Anisinodus crinitus n. sp.

Diagnosis (including features of family rank). Larva elongate, soft-bodied, eucephalic. Head capsule broad and strongly sclerotized. Body without projections, with distinct crowns of claws, anterior one(s) near hind margin of head, posterior one(s) at caudal end; probably crowns of claws at apex of anterior and posterior parapod(s). Abdominal segments not annulate, densely setose; last segment with a fringe of setae on probable lobes.

Etymology. The genus is named after its occurrence in the Anisian and after the Latin name *nodus* = knot. Gender masculine.

Remarks. This fossil is attributed to the Chironomoidea based on the presence of anterior and posterior crown of claws on the prothorax and the last abdominal segment, but a unique combination of characters and the difficulties in their interpretation preclude assigning the new genus to any of the known families (for details see Discussion).

Anisinodus crinitus n. sp. (Figs 5, 6, 9A)

Holotype. Larva 6187a± (Arzviller).

Etymology. The species name refers to the hairy caudal end (from Latin *crinitus*=hairy).

Description. Larva length *ca* 4.5 mm. Antenna, eye spots and mouthparts not visible. Anterior parapods with brown claws, at least four in number. Structure of densely setose abdominal apex obscure. Posterior parapod claws (cl) at least five in number, subequal to the anterior ones, thick, curved, dark brown. Abdomen only slightly expanded towards apex around segment V to VII. Sclerotized spiracles (sp) supposed on segment VIII surrounded by relatively long setose slender lobes (ll) or processes. Supposed spiracular field surrounded by fleshy lobes with numerous setae at the margin; presumably, lobes broad, dorsal(?) much longer than the ventral ones.

Remarks. Due to the state of preservation one cannot be sure in the structure of the abdominal apex. We suppose that the larva is twisted and on Figs 5C, 6C there is a ventral view with crowns of claws (one is obvious and the second part is preserved as only tips of claws), relatively long slender lobes positioned almost laterally and short fleshy densely setose lobes. On Figs 5A, 6A there is a dorsal view with sclerotized spiracles and longer dorsal setose fleshy lobes (however another interpretation is possible). We interpreted the setose structure(s) visible beyond posterior claws as fleshy lobe(s) supposedly arising from the penultimate segment, because the crown of claws must be in terminal position for locomotion, so the structure(s) cannot represent the ultimate segment. However, a combination of posterior crown of claws (the number of parapods is unclear and even their presence is not obvious) with lobes is unknown in recent Diptera.

On the same slab there is also a poorly preserved dipteran adult, numbered 6187b± without antennae, wings and legs, so certainly allochtonous.

Nematocera incertae sedis

There are further pupae and larvae from the Grès à Voltzia, but they are not well enough preserved to be classified even up to the infraorder level. Indeed, many important features, such as respiratory horns, are missing in all these pupae, and they may be identified only up to the order (5430/5431 and 9098± from Arzviller, 9099 from Bust). Some other pupae are of doubtful affinities (9070, 9090 and 9102b from Arzviller possibly do not belong to Diptera). Nevertheless, several other immature specimens are worth to be described and discussed because of their diversity and for the presence of several interesting characters.



Figure 5

Photographs of the holotype larva of *Anisinodus crinitus* **n. gen., n. sp.** from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). **A–B**, detail of abdominal apex and head capsule on part from Fig. 9A; **C–D**, abdominal apex and anterior margin of thorax on counterpart. Scale bar = 0.1 mm. cl – crown of claws, ll – long lobe, sp–spiracle.

Pupae

Gen. sp. 1 (Figs 3D, 4D, 7C)

Material examined. Pupa 9080± (Arzviller).

Description. Pale pupal exuviae, *ca* 5.5 mm long, wing sheath 1.7 mm long. Dorsum of dark cephalothorax smooth, without large setae. Abdominal tergite I somewhat wider than the narrow metanotum, all segments subequal, with tergites more strongly sclerotized than sternites. Abdominal segments without secondary segmentation, with one row of relatively large, sparse spines along posterior margin (8 spines per 0.5 mm).

Remarks. Many observable characters are similar to those of *Voltziapupa* spp., but the pale spines are larger and sparser. Important features such as the respiratory horns, the head structure and the leg pattern are unknown, so it is impossible to be sure that these types of pupae are congeneric or not.

Gen. sp. 2 (Figs 3E, 4E, 7D, 8A)

Material examined. Pupa 9067 (Bust). Description. Pale pupal exuviae, 4 mm long and 1 mm wide,



Figure 6

Line drawings of the holotype larva of *Anisinodus crinitus* **n. gen., n. sp.** from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). **A–B,** abdominal apex and head capsule on part; **C–D,** abdominal apex and anterior margin of thorax on counterpart. Scale bar = 0.1 mm. cl – crown of claws, ll – long lobe, sp – spiracle.



Photographs of the Diptera pupae from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). A-B, *Voltziapupa cornuta* **n. gen., n. sp. A**, paratype 9106 (Arzviller). **B**, holotype (Arzviller). C–H, Nematocera *incertae sedis*. **C**, gen. sp.1: 9080 (Arzviller). **D**, gen. sp.2: 9067 (Bust). **E**, gen. sp.3: 9072 (Arzviller). **F**, gen. sp.5: 9086 (Arzviller). **G**, gen. sp.6: 9093 (Arzviller); **H**, gen. sp.4: 9074 (Arzviller). Scale bar = 1 mm. fh – frontal horn, ls – leg sheath, mc – middorsal cleft, mtn – metanotum, rh – respiratory horn, ws – fore wing sheath, arrow marked strip (see the text).

with one row of minute and very dense spines located along posterior margins of tergites (some 40 spines per 0.5 mm). Abdomen with possibly a secondary segmentation or only wrinkled.

Remarks. The habitus and the row of dense spines do not contradict the assignment of this exuviae to one more species of *Voltziapupa* **n. gen.** However, since the respiratory horns, the head structure and the leg pattern are not preserved, it is not possible to conclude. Moreover, the secondary segmentation or wrinkled cuticle is unknown in any other pupa from the Grès à Voltzia (it does not seem to be related to the state of preservation).

Gen. sp. 3 (Figs 7E, 8B)

Material examined. Pupa 9072 (Arzviller).

Description. Incomplete pupa (abdominal apex not preserved), about 2.3 mm long (preserved part without intersegmental areas) and 0.5 mm wide, slender, elongate-cylindrical, possibly exarate. Head distinct, possibly prognathous, narrower than thorax, separated from thorax by a constriction; region of developing compound eye slightly convex. Abdomen consisting of wide distinct segments, tergites more sclerotized than sternites, posterior margins of tergites III–VI with a row of spines. Arrangement of leg sheaths not visible.

Remarks. Some of these features, such as the slender, elongate-cylindrical pupa without respiratory horns, with a prognathous head and a convex region of developing eye, are known in the recent Nymphomyiidae, but in this family the thorax is more elongate and the leg sheaths are arranged in a peculiar way (Keith et al. 1981). Unfortunately the latter is unclear in the specimen 9072. Pupae of some other nematoceran families (Tanyderidae and some Chironomidae) are similar in the body outlines and proportions. They often have very small (or lost) respiratory horns, but the head is always hypo- or opisthognathous.

Gen. sp. 4 (Figs 3F, 4F–4G, 7H, 8E)

Material examined. Pupa 9074± (Arzviller).

Description. Pupa of female, 6.8 mm long (with intersegmental areas). Cephalothorax dark, abdomen pale. Dorsum of cephalothorax gibbous, smooth, with long setae forming lozenge (possibly chaetotaxy of adult visible under cast skin). Wing sheaths 2 mm long, reaching mid-length of body, *i.e.* segment IV of abdomen, split of exuviae running along midline from head to well-developed metanotum. All leg sheaths (ls) directed



Figure 8

Line drawings of the Diptera pupae of Nematocera *incertae sedis* from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). **A**, gen. sp.2: 9067 (Bust). **B**, gen. sp.3: 9072 (Arzviller). **C**, gen. sp. 5: 9086 (Arzviller). **D**, gen. sp.6: 9093 (Arzviller). **E**, gen. sp. 4: 9074 (Arzviller). Scale bar = 1 mm.

backwards, lying parallel to one another, not covering each other and ending approximately level with apex of wing sheaths. Leg sheaths unequal in length: fore legs the shortest, ending before wing sheath apices, and hind leg the longest; distal parts of mid and hind tarsi curved medially. Abdominal segments subequal, about 1.3 mm wide, without secondary segmentation, with numerous setae (possibly adult pubescence visible through cast skin). Row of dark spines located along posterior margins of tergites not very dense, about 10–12 spines per 0.5 mm. Three sclerotized spermathecae visible near boundary of segment VII. Genitalia sheaths without any processes and setae.

Remarks. This pupa differs from *Voltziapupa* **n. gen.** in the shape of the genitalia sheaths and perhaps in chaetotaxy of the thorax and abdomen. The thorax with a definite bristle pattern may be a character of generic value. For example, in Anisopodidae, the thorax of *Sylvicola* Harris 1780 is hairy dorsally, whereas it is bare in *Olbiogaster* Osten Sacken 1886 (Krivosheina 1997). However, the difference in shape of the genitalia sheaths indicates another family affinity.

Gen. sp. 5 (Figs 7F, 8C)

Material examined. Pupa 9086± (Arzviller).

Description. Small pupa, about 2.8 mm long (with intersegmental areas) and 0.7 mm wide, with large adult eye. Leg sheaths (ls) of subequal length (at least 2 pairs), lying side by side, much longer than wing sheaths, reaching abdominal segment V. Abdominal segments wide, without secondary segmentation.

Remarks. Such pattern of leg sheaths is most typical



Figure 9

Photographs of the dipteran larvae from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). Comparison with larva of the recent psychodid *Clytocerus rivosus* (Tonnoir, 1919). **A**, total view of holotype of *Anisinodus crinitus* **n. gen., n. sp.** (Arzviller) on part. **B**, abdominal apex of recent *Clytocerus rivosus* (Tonnoir, 1919). C–D, gen. sp. 7: 9073 (Vilsberg). **C**, total view; **D**, apex of abdomen. E–F, gen. sp. 8: 9347 (Adamswiller); **E**, total view on part; **F**, abdominal apex on counterpart. Scale bar = 1 mm except for Figs 9B, 9D, 9F enlarged (not to scale).

of the Tipulomorpha, but also known in the recent Ptychopteridae and Mycetophilidae (pers. obs.) and as an exception – in the derived Chironomidae (*Stictocladius* Edwards 1931; Brundin 1966).

Gen. sp. 6 (Figs 7G, 8D)

Material examined. Pupa 9093± (Arzviller).

Description. Pale pupal exuviae, *ca* 4 mm long, without any traces of secondary segmentation, sclerotization and chaetotaxy. Cephalothorax with prominent anterior median protrusion. One pair of leg sheaths (ls) much longer than wing sheaths and possibly than other leg sheaths being not visible.

Remarks. The lack of elongate cylindrical respiratory horns and the presence of a protrusion in the centre of the head disc resemble the outlines of some recent



Figure 10

Line drawing of the dipteran larvae of Nematocera *incertae sedis* from the Grès à Voltzia (early Middle Triassic) of the Vosges (France). **A**, gen. sp. 7: 9073 (Vilsberg) apex of abdomen from Fig. 7C. B–C, gen. sp. 8: 9347 (Adamswiller): **B**, anterior half on part; **C**, apex of abdomen on counterpart. Scale bar = 1 mm.

dipteran pupae with adjacent, wide and low respiratory horns, *e.g.* the crane flies *Dicranomyia* Stephens 1829 (per. obs.) and several Brachycera, *e.g.* Bombyliidae (Brauns 1954). However this homology is not obvious and other possible homologies are: (1) an unpaired anterior projection of the cephalothorax is known in *e.g.* Scatopsidae (Smith 1989) and Bibionidae (Brauns 1954); (2) a frontal apotome of the Chironomidae or an operculum of the Ceratopogonidae, which has a tendency to get detached from the exuviae.

The strip visible on the wing sheath of specimen 9093 (marked by an arrow on Fig. 7G) may be either the trace of the wing sheath venation or that of the recurved hind tarsus. The long and curved leg sheaths visible in this exuviae may be interpreted as the middle or hind pair previously bent under the wing sheaths and having stretched out after the emergence, so the position of leg sheaths is also similar to that which can be observed in the exuviae of many recent longlegged Chironomidae, whose pupa is characterized by apical parts of leg sheaths free, weakly sclerotized and curved anteriorly under the wing sheaths. In exuviae, leg sheaths can change their positions and be situated outside the wing sheaths. In contrast to this, in most of the other groups of Nematocera, the pupae with long leg sheaths (e.g. Ceratopogonidae, Mycetophilidae, Limoniidae, Ptychopteridae, etc.) are more sclerotized or/and glued to each other and to the body, hence they do not change the position after the eclosion of adult (Przhiboro, pers. obs.).

In the aquatic pupae of recent Nematocera there is a tendency to the reduction of the sclerotization and chaetotaxy similar to that observed in the pupa 9093, so this pupa is possibly aquatic one. Thus, the specimen 9093 possesses a complex of characters typical of the Culicomorpha, but since the "culicomorph" features are dubious and can be interpreted alternatively, we refrain from assigning this pupa to the Culicomorpha.

Larvae

Gen. sp. 7 (Figs 9C–9D, 10A)

Material examined. Larva 9073± (Vilsberg).

Description. Larva elongate, *ca* 5 mm long without head (not preserved). Thoracic segments probably dorsoventrally flattened. Abdominal segments possibly with secondary segmentation or with sclerotized tergal plates, pubescent (with numerous short setae). Siphonal segment provided with long setose appendages (only one visible).

Remarks. A siphonal segment strikingly similar in shape and structure occurs in the larvae of the recent family Psychodidae (subfamily Psychodinae), *e.g.* in

Clytocerus rivosus (Tonnoir 1919) (Fig. 9B), usually forming a more or less elongate complex, with hind stigmata close together and surrounded by two pairs of short or long setose appendages (Wagner 2000). A similar shape of the last abdominal segment is known also in many Limoniidae. The elongate body with a secondary segmentation is also a peculiarity of the Psychodinae, but in the latter it is much more pronounced, with ring-shaped pseudosegments that usually bear heavily sclerotized dorsal plates.

Secondarily divided segments are also known in the Trichoceridae, Leptoconopidae, Keroplatidae, Mycetobiidae and Anisopodidae. However, among these families, only the Trichoceridae have similar terminal segment with four medium-sized lobes that are sclerotized medially and fringed with short fine setae; smaller unsclerotized lobes are known in anisopodid genus *Sylvicola* (Krivosheina & Mamaev 1967). At the same time, tergal structures may look somewhat similar to crawling welts, which are well developed on tergites *e.g.* in many recent Limoniidae (*Antocha* Osten Sacken 1860, *Elliptera* Schiner 1863, *Dicranomyia, etc.*; Oosterbroek & Theowald 1991). However, most probably the specimen 9073 belongs to the Psychodomorpha *sensu* Hennig.

Among the rare psychodomorph larvae known from the Jurassic, the larva of *Eopericoma zherichini* Kalugina 1985 from Uda, Transbaikalia, was tentatively assigned to Psychodinae (Kalugina & Kovalev 1985).

Gen. sp. 8 (Figs 9E–9F, 10B–10C)

Material examined. Larva 9347± (Adamswiller).

Description. Larva large, about 21.5 mm long, with sclerotized head. Each thoracic segment with one wide sclerotized dorsal plate. Nine abdominal segments, not annulated. Structure of the abdominal apex obscure; probable tracheal trunks with anastomosis and a spiracle visible on the dorsal prominence.

Remarks. It is uncertain if sclerotized dorsal plates were present on abdominal segments: they were either absent or obscured by decaying guts. Sclerotized dorsal plates on all the body segments are characteristic of many recent Psychodidae. At the same time, many xylobiontic insect larvae living under the bark have thoracic segments dorsally sclerotized and anterior body end tapered (*e.g. Xylophagus* Meigen 1803 (Xylophagidae). Possibly, the larva 9347 was also xylobiontic. Additionally, its abdominal apex seems to look like that of recent Psychodidae and, especially, of Scatopsidae, which have tubular posterodorsal processes each bearing a spiracle, and posteroventral lobes (Krivosheina & Mamaev 1967; Smith 1989).

Xylobiontic larva of *Plecia thulinigra* Hardy 1961 (Pleciidae) is also somewhat similar in having a sclerotized plate on the first thoracic tergite and long posterodorsal processes on the last abdominal segments (Krivosheina & Mamaev 1967). Another interpretation of the abdominal apex structure in the larva 9347 is also possible: in some xylobiontic larvae (*Xylophagus, Hyperoscelis* Hardy & Nagatomi 1960 and *Synneuron* Lundström 1910 (Canthyloscelidae)), the spiracular field of the last abdominal segment is situated posterodorsally and supplied with two strong sclerotized posterior hooks curved dorsally (Krivosheina & Mamaev 1967).

Discussion

The affinities of the immature Diptera from the Grès à Voltzia are very difficult to determine due to lack of other data on Triassic dipteran immatures and their rarity in the Jurassic, except for the Culicomorpha (Kalugina & Kovalev 1985; Kalugina 1986; Kalugina 1989; Lukashevich 1995). Moreover, it is not easy to find affinities of the pupae from the Grès à Voltzia, even at the infraorder level.

The occurrence of Culicomorpha in the Middle Triassic

The possible presence of immature Culicomorpha in the Grès à Voltzia of the Vosges was one of the important questions. Among the adult Diptera described by Krzeminski and Krzeminska (2003) from the Grès à Voltzia there are no representatives of the Culicomorpha, 'the most aquatic' infraorder, whereas the environment was quite favourable for aquatic insects (Sinichenkova et al. 2005). Finds of Culicomorpha in the Triassic are extremely rare: only few adults are known from the Upper Triassic (Krzeminski & Jarzembowski 1999, Blagoderov et al. 2007). Even in the beginning of the Jurassic, Culicomorpha were not as numerous as they became later. No culicomorph immatures are known from the Upper Triassic and the Lower Jurassic of Europe and Asia whereas they become common in the Middle-Upper Jurassic and the Cretaceous. Moreover we do not know pupal habitus of the earliest chaoborids (Rhaetomyia Rohdendorf 1962) and chironomids (Aenne Ansorge 1999). Thus the chance to find them in the Grès à Voltzia seemed to be low. However, one of the larvae found by Grauvogel, Anisinodus n. gen. proves that the culicomorph superfamily Chironomoidea has already existed in the early Middle Triassic.

Wood & Borkent (1989) following Hennig (1973) considered the presence of a prothoracic proleg, crowned

apically with rows of hooklets as a synapomorphy of the Chironomoidea. Later a prothoracic proleg composed of a transverse, membranous undivided ridge with a single, transverse row of minute hooks was found in the first instar larva of *Corethrella appendiculata* Grabham 1906 (Corethrellidae, Culicoidea; Borkent & McKeever 1990). However parapods (prolegs, pseudopods of some authors) on the prothorax and the terminal segment, usually with characteristic groups of claws, seem to be a unique character of the superfamily Chironomoidea (Teskey 1981), hence we place *Anisinodus* **n. gen.** in this superfamily. Due to uncertainty of interpretation of some fossil structures we prefer to retain this important larva without familial assignment within the Chironomoidea.

The eucephalic head capsule (complete and nonretractile into the thorax) is doubtless plesiomorphic for Diptera and characteristic of most families of Nematocera, including the Trichoceridae, whereas all the Tipuloidea larvae are hemicephalic. The shape and degree of sclerotization of the head capsule is similar to many recent larvae of Nematocera, including many Ceratopogonidae and Chironomidae.

In the Chironomoidea functional, sclerotized posterior spiracles (supposed in the new genus) are present only in some Podonominae (Archaeochlus drakensbergensis Brundin 1966, Chironomidae; Brundin 1966) and in Thaumaleidae, where they open into a transverse cleft between fingerlike processes arising just behind these spiracles on the abdominal segment VIII (Smith 1989). The long setose slender lobes of the Triassic larva are in a very similar position just behind the spiracles; it is clear after combining the drawings of the part and counterpart, Figs 6A, 6B. They are similar to the cylindrical procerci with long apical setae but not yet transformed into these. Moreover, the larvae of Thaumaleidae possess unpaired anterior and posterior parapod with small setae or claws but their dorsal areas are sclerotized darker, and the anal papillae are the most terminal part of the body (terminal lobes absent). Such distinctly hairy abdominal apex visible distal to the crown of claws in the Triassic larva (and difficult to interpret – fleshy lobes?) is unknown in any family of Chironomoidea.

Members of the Chironomidae usually possess anterior and posterior parapods with crown of large claws in the apical position. Bilobate anterior parapods and posterior parapods consisting of a group of claws and anal segments with anal gills (sometimes broad, distal to claws) are known in Ceratopogonidae Forcipomyiinae (posterior parapods are also developed in another subfamily, Dasyheleinae). However, gills are not setose and can not be compared with lobes. At first sight, the general habitus of *Anisinodus crinitus* **n. gen., n. sp.** excluded its relationship to the Simuliidae, since the larva seems to be not sessile, the head capsule is without a pair of conspicuous mouthbrushes (labral fans) and the anal segment is lacking a circlet of minute hooked spines. However, the slightly expanded abdomen of the fossil possibly displays a tendency known among the Chironomoidea only in the Simuliidae whose larval abdomen is conspicuously swollen distally. Alternatively, swelling of the larval abdomen can be an artifact caused *e.g.* by decaying gut contents.

The only known fossil simuliid larvae are much younger, being from the Early Cretaceous of Australia (Jell & Duncan 1986). They show excellently the head and body shape, and cephalic fans and pseudopods, just as these are in present-day larvae. Moreover, the oldest described simuliid pupa Simulimima grandis Kalugina 1985 $(J_{1/2}, Siberia)$ "has features characteristic of the modern *Prosimulium* pupa, including the usual arborescent gill, long tail-hooks and abdominal spinecomb" (Crosskey 1990: 59). So in the Middle Jurassic simuliids seem to be already well adapted for life in running water, and surely this family has a long history. One can suppose that Anisinodus crinitus n. gen., n. sp. is close to ancestors of both the Chironomidae-Ceratopogonidae and the Simuliidae lineages, yet without their apomorphies (fingerlike setose processes arising just behind posterior spiracles are neither modified into chironomid procerci nor lost as in Simuliidae).

Only one pupa among Nematocera inc.sed. of the Grès à Voltzia (gen. sp. 6; Figs 7G, 8D) possesses several characters typical of Culicomorpha (see above), but since the "culicomorph" features can be interpreted alternatively, we refrain from assigning this pupa to the Culicomorpha. All we can be sure about is that pupae having typical culicomorph habitus and features (long leg sheaths turned under the wing sheaths, spindleshaped or trumpet-like thoracic horns with reticulated surface) have not been found in the Grès à Voltzia whereas they are widespread in Middle-Upper Jurassic deposits. It is noteworthy that insect egg clusters occurring abundantly in the Grès à Voltzia have been compared to those of the Chironomidae, as well as to those of Trichoptera and Odonata (Gall & Grauvogel 1966; Gall, 1971; Grauvogel-Stamm & Kelber 1996), and the latter attribution seems the most plausible (Nel et al. 1996).

Affinities of Voltziapupa n. gen.

The temptation to assign the most abundant and well-preserved pupae to *Grauvogelia arzvilleriana*, described from the isolated wings from the Grès à Voltzia of the Vosges (Krzeminski et al. 1994), and to consider them as two developmental stages of the same insect, was great. Indeed, both mostly occur in the same locality (Arzviller) and in the same lens. Moreover, the fact that the size of the wings of G. arzvilleriana (4-4.5 mm) is twice as long as the wing sheaths of these pupae (about 2 mm) made this hypothesis plausible. For example, in the Ptychopteridae the wing is nearly twice as long as the pupa wing sheath (Lukashevich 1995). However, these arguments remain tenuous and the only way to be more or less sure that these pupae belong to G. arzvilleriana, would be to know if their venations are similar. Unfortunately, the venation of the wing sheath visible only in the holotype (Figs 1A, 2A) is not well enough preserved to arrive at any conclusion. Therefore the most abundant pupae occurring in the Grès à Voltzia have been assigned to Voltziapupa n. gen.

Grauvogelia was described as a member of the family Grauvogeliidae in the infraorder Grauvogeliomorpha Krzeminski, Krzeminska & Papier 1994. Later, one of us (Lukashevich & Shcherbakov 1999) proposed to keep grauvogeliids (like other "Diarchineura") in the Psychodomorpha and to consider them as a superfamily Grauvogelioidea close to the Ptychopteroidea.

The fact that the characters of *Voltziapupa* **n. gen.** such as the relative length and arrangement of the leg sheaths, the shape of the thoracic horns, the armature of the abdomen and the structure of the genital sheath, occur in unusual combinations not recorded in any extant family, led us to consider the new genus as a member of Grauvogeliidae but with a question mark in order to indicate the uncertainty about this systematic position.

Comparative analysis of the features of *Voltziapupa* n. gen.

Some features of *Voltziapupa* **n. gen.** such as more or less developed frontal horns, very elongate respiratory horns with an apical widening, leg sheaths directed backwards and not superimposed but lying subparallel to each other, with fore legs the shortest, deserve to be discussed in more detail.

Leg sheaths lie parallel to one another, side by side, in all the Tipuloidea pupae as well as in several other nematoceran families, *e.g.* Tanyderidae, some Ptychopteridae, Mycetophilidae, Cecidomyiidae (pers. obs.) and as an exception – in Chironomidae (*Stictocladius* Edwards 1931; Brundin 1966). This character is considered as one of the synapomorphies of the Tipuloidea (Oosterbroek & Theowald 1991). However, in all extant Tipuloidea as well as in other dipterans mentioned above, the leg sheaths are much longer than the wing pads (even when the length of leg sheaths is much shorter than half of pupal body). The leg sheaths subequal in length to the wing pads are typical of the recent members of the Psychodidae (most similar to Voltziapupa n. gen. in the habitus), Trichoceridae and Anisopodidae (Psychodomorpha sensu Wood & Borkent but three various infraorders sensu Hennig), and are known in an aberrant and apomorphic orthocladiine genus Lopescladius Oliveira 1967 (Chironomidae, Brundin 1966) but they are superimposed in all mentioned cases. However pupae of Voltziapupa n. gen. display an unusual combination of subparallel leg sheaths that are relatively short (subequal) compared with the wing pads. It is difficult to discuss the possible primitiveness of this combination due to the presence of other combinations among the Anisian pupae. Indeed in the specimen 9086 (gen. sp. 5; Figs 7F, 8C), which is included in the Nematocera inc. sed., the possibly parallel leg sheaths are much longer than the wing sheaths. Moreover, there is a hypothesis about the exarate pupae of Voltziapupa n. gen. (i.e. with appendages free from the body, see above).

Regarding the relative length of the leg sheaths, in the Mecoptera including the Nannochoristidae (Pilgrim 1972) and in the majority of the Diptera Nematocera including the Tipuloidea, the sheaths of hind legs are the longest and the fore pair is the shortest (although in several limoniid subfamilies, some species possess leg sheaths of equal length, or the middle leg sheaths are the shortest; Oosterbroek & Theowald 1991). Therefore a pattern of *Voltziapupa* **n**. **gen.** with the sheaths of hind legs being the longest is a groundplan without doubts.

The mesothoracic respiratory horns are present in most of the Tipuloidea, Psychodoidea, Ptychopteroidea and in a number of other families of Nematocera and Brachycera-Orthorrhapha, whereas they are absent in the Mecoptera pupae and weakly developed in the Trichoceridae (Brauns 1954). The elongate, more or less cylindrical or somewhat flattened respiratory horns are considered to be the groundplan condition in the Tipuloidea (Oosterbroek & Theowald 1991). *Voltziapupa* **n. gen.** with rather thin and long respiratory horns shows just the same pattern. Among the recent Diptera, long thin horns are most typical of semiaquatic pupae of all Ptychopteridae and some Limoniidae (limnophiline genera Paradelphomyia Alexander 1936, Pseudolimnophila Alexander 1919, Pilaria Sintenis 1899, Neolimnomyia Séguy 1937 and Ulomorpha Osten Sacken 1869). All of them are hygrophilous with larvae inhabiting moist or semiaquatic shore habitats with soft substrate (fine-particulate detritus, mud, sand; Brindle 1967; Savchenko 1986).

Elongate respiratory horns are also described in semiaquatic or aquatic pupae of some Psychodidae (e.g. Tinearia alternata (Say 1824)), Ceratopogonidae (e.g. members of the genera Dasyhelea Kieffer 1911 and Culicoides Latreille 1809) and Chironomidae of the subfamilies Orthocladiinae and Chironominae (Przhiboro, pers .obs.). Rather long and thin horns (comparable with the body in length) are known in some Dolichopodidae inhabiting sandy and muddy substrates in the sea intertidal zone, e.g. Paraphrosylus praedator (Wheeler 1897) and Machaerium maritimae Haliday 1832 (Saunders 1928; Smith 1989). However, as far as we can judge from the literature (e.g. Glukhova 1979; Savchenko 1986; Langton 1995), there is no absolute correlation between the larval habitats and the degree of development of pupal respiratory horns, and the tendencies in different families (e.g. Limoniidae and Chironomidae) may be quite different. Long respiratory horns comparable with the length of wing pads are also known in terrestrial dipterans, e.g. in Tipuloidea (relatively primitive pediciid mycetobiont Ula Haliday 1833, limnophiline xylobionts Epiphragma Osten Sacken 1860 and Austrolimnophila Alexander 1920) and Sciaroidea (many Cecidomyiidae, especially the members of the supertribe Asphondyliidi - Möhn 1961). As a rule, the horns of the terrestrial pupae are pointed or at least not widened apically. Rarely, long horns comparable with the body length are developed in aquatic pupae that are able to live under the water surface [ribbon-shaped horns in Dasyhelea modesta (Winnertz 1852), Ceratopogonidae (Przhiboro, pers. obs.); lash-shaped horns in Aphroteniella filicornis Brundin 1966, Chironomidae (Brundin 1966)].

Since many wings of the Anisian dipterans demonstrate a combination of primitive and advanced features, one can suppose that the same occurred in the pupae of the Triassic extinct families and that their long respiratory horns with an apical widening represent probably a specialization, and not a primitive feature.

The frontal horns (or cephalic crest in the Tanyderidae and cephalic tubercles in the Chironomidae) are known in the pupae of many extant families in different infraorders of Nematocera (*e.g.* Tanyderidae, pupae of many extant families in different infraorders (e.g. Tanyderidae, Limoniidae, Chironomidae, Sciaridae, Cecidomyiidae, Empididae and Asilidae; Crampton 1930; Brauns 1954; Milhn 1961; Brindle 1967; Trehen 1971; Langton 1995, etc.). These pupae include aquatic, semiaquatic and terrestrial forms. In different families, these structures can be used for locomotion in the substrate or for penetrating the cocoon wall, host plant tissues or other substrate before the eclosion of the adult (Felt 1925; Brauns 1954). Möhn (1961) discussed the evolutionary trends of the development of frontal horns ("*Scheitelstacheln*") in Asphondyliidi (Cecidomyiidae) and found that in different tribes of this supertribe the shape of the horns and the degree of their sclerotization correlate strongly with the tendency to pupate within galls and with the hardness of the gall wall. Langton (1995) suggested that cephalic tubercles in the Chironomidae may play different roles, including a sensory function (shorter tubercles with a sensory seta) and a protective one (longer or spinose tubercles that can deter access to the pupal tube by other organisms).

In the Tanyderidae, a pair of well-developed frontal horns is present in *Protoplasa* Osten Sacken 1859 (Alexander 1930) and *Protanyderus* Osten Sacken 1877 (Knight 1964), but is absent in *Peringueyomyina* Alexander 1921 (Wood 1952). Crampton (1930: 85) has supposed that "these horns may serve to protect the pupa in some way from the sand and small rocks of their habitat". Larvae of the three tanyderid genera mentioned above as well as several species of the limoniid genus *Hexatoma* Latreille 1809 subgenus *Eriocera* Macquart 1838 with similar frontal horns were collected from the sand, the mud or the gravel, mostly at the water margins in streams or rivers with various current velocities (Brindle 1961; Exner & Craig 1976; Savchenko 1986).

Mode of life of Voltziapupa n. gen.

The life near the shorelines of large rivers with slow current, which was reconstructed by Sinitshenkova *et al.* (2005) for the immature mayflies (particularly *Voltziaephemera* Sinichenkova *et al.* 2005 and *Triassonurus* Sinichenkova *et al.* 2005) found abundantly in the Grès à Voltzia, may be also that of the immature Diptera, whose pupae are found in the same beds as these mayflies. Possibly, the dipteran larvae burrowed in the sand or the gravel in shallow lotic habitats as the burrowing mayfly nymphs and later migrated towards drier areas for pupating, as do many limoniid hydrobionts (not only *Hexatoma*) and probably also the tanyderids (Wood 1952; Exner & Craig 1976; Savchenko 1986).

However, most probably, the larvae were semiaquatic and developed within the water margin zone, as most "aquatic-dependent" immatures of recent dipterans. This assumption is made mostly by analogy with the recent Diptera. Larvae are semiaquatic in almost all the recent Diptera whose semiaquatic pupae have similar respiratory horns. Immatures in over 40 recent dipteran families are known to develop in semiaquatic habitats, but in most of these families larvae depend on the atmospheric air, and, as a rule, they cannot

survive at the bottom of reservoirs or when submerged under the water surface (Przhiboro, pers. obs.). In many families being rich in the number of species that develop in the water margin zone, aquatic larvae not dependent on atmospheric air are virtually unknown (e.g. Psychodidae, Ptychopteridae, Sciaridae, Stratiomyidae, Dolichopodidae etc.). In many other species-rich families in the water margin zone (e.g. Tipulidae, Limoniidae, Tabanidae, Muscidae), the larvae of only some species develop in aquatic habitats without access to the atmospheric air, and most of them are confined to the running waters rich in oxygen, either fast-running or cold. However, judging from the reconstruction of the landscapes (Gall 1971, 1985), the Grès à Voltzia Formation corresponds to a deltaic area with wet warm climate, and thus the semiaquatic life mode of the larvae is most probable.

In any case, pupation of *Voltziapupa* spp. probably occurred in the water margin zone or in drier zones above the waterline (in shore debris, litter or soil), as observed virtually in all the recent dipterans with semiaquatic larvae and in many ones with aquatic larvae, e.g. in Tipuloidea (Pedicia Latreille 1809, Hexatoma etc.) and Ceratopogonidae (Palpomyia Meigen 1818, Mallochohelea Wirth 1962 etc.; e.g. Brindle 1961; Glukhova 1979, Przhiboro, pers. obs) Many semiaquatic air-dependent larvae of recent Diptera in various families also prefer drier places for pupation (e.g. Dixidae, Ceratopogonidae, Psychodidae, Stratiomyidae, Tabanidae) (Przhiboro, pers. obs.). In the only extant mecopteran family Nannochoristidae with aquatic larvae, they also move out of water to pupate in a damp substrate, e.g. in wet moss (Pilgrim 1972).

A combination of some morphological features of *Voltziapupa* spp. also suggests that they were semiaquatic, namely, the following features: 1) the well-sclerotized body; 2) the relatively well-developed armature on the abdominal segments (transverse rows of spines or large single spines on many segments and large spines on the last segment); 3) the long unbranched respiratory horns with apical widening (see above).

The first two features are typical of semiaquatic and terrestrial pupae of dipterans whose larvae do not build a cocoon or silken tube before the pupation. These pupae are usually motile and are able to crawl actively and to change their position in the substrate at least during the first days after pupation. In the aquatic pupae and in the pupae of cocoon- or tube-builders, the sclerotization and armature are usually weaker (Przhiboro, pers. obs.).

The different habitats that result in different burial chances for the larvae and the pupae may partly explain the rarity of the dipteran larvae in the Grès à Voltzia, whereas the pupae, especially their empty exuviae, are relatively abundant. They were probably washed out from the banks by high water or drifted away by the current after their emergence and buried at a distance from their pupation habitat, e.g. in a lake at the river mouth or in a floodplain lake affected by running waters in the periods of flood. According to Sinitshenkova et al. (2005) a lot of specimens of the mayfly Voltziaephemera are macerated so one can conclude that they are allochthonous (not buried in their habitats but drifted) as well as the dipteran pupae. In this case a rarity of larvae is explained easily – larvae inhabiting semiaquatic substrates usually do not drift, whereas pupae usually leave the substrate and crawl on to its surface before the adult emergence. In addition, pupal exuviae are usually much strongly sclerotized than the larval ones and have much better chances to retain safe when drifting. Numerous aquatic larvae usually are preserved at least as larval heads in many Jurassic localities, however head capsules are not found on the slabs from the Grès à Voltzia.

Kovalev (1983b) discussed the lack of immature Diptera in the Triassic and the loss of the legs by the dipteran larvae. Basing on a resemblance of the wings of the Triassic Diptera and those of the recent Tanyderidae and considering the aquatic mode of life as being plesiomorphic for the order, he hypothesized that the larvae of the first true flies bored the surface layers of the submerged rotting wood, like those of the recent Australian Eutanyderus Alexander 1928 (Colless & McAlpine 1970). Unfortunately, the pupal morphology and the place of pupation of the Australian tanyderids have not been described, and their finds are extremely rare. Their exuviae have never been caught by drift netting, so it is supposed that either the larvae do not pupate in the water or that the exuviae remained in the larval habitat (i.e. in the immersed wood; P.S. Cranston, pers. comm. 2009). Such a model does not agree with the Triassic immatures from the Grès à Voltzia of the Vosges. Indeed, the numerous pupal exuviae occurring in some lenses (as in some Arzviller lenses, where only exuviae were found) suggest that the pupae lived in aquatic or semiaquatic habitats.

Conclusion

As shown in the present study, immature Diptera were preserved in the early Middle Triassic Grès à Voltzia Formation, and the pupae were rather diversified, quite as the adult Diptera from these strata, whereas the larvae are rare. Such a situation is unique for the Triassic (indeed, up to now no immature Diptera were recorded from the other Triassic localities). In the most numerous pupae, *Voltziapupa* **n. gen.**, plesiomorphic characters are combined with possibly derived ones: elongate cylindrical respiratory horns, antennae of at least 14 segments, leg sheaths parallel, not superimposed, ending level with the wing sheath apices, and relatively developed pupal armature. Based on the comparison with recent Diptera, we suggest a semiaquatic mode of life in these pupae, and aquatic or semiaquatic habitats of their unknown larvae. This study provides the earliest record for the infraorder Culicomorpha and demonstrates that Chironomoidea have already existed in the early Middle Triassic.

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