The Oldest Aphid Insect from the Middle Triassic of the Vosges, France

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JACEK SZWEDO and ANDRÉ NEL

A new family Vosegidae is described for *Vosegus triassicus* gen. et sp. nov. from the Anisian (early Middle Triassic) Grès à Voltzia Formation of the Vosges (north-eastern France). This is the oldest Aphidomorpha presenting the combination of characters as: elongate and tapered pterostigma with straight posterior margin, thick common stem of veins Sc+R+(M)+CuA, arcuate RP separated well basad of pterostigma base, three-branched M with free base, CuA forked, veins not differentiated in their thickness. The morphological characters presented by *Vosegus* are spread among the different extinct and extant lineages of Aphidomorpha, but the combination presented is unique. The relationships of this new family to other Triassic Sternorrhyncha are discussed, concluding its placement in Aphidomorpha: Triassoaphidoidea. The specificity of Grès à Voltzia fossil site in respect to early evolution of aphids is presented, with two competing explanations for size diminution, considering the Early Triassic biotic recovery versus the correlation between early aphid diversification and the exploitation of new niches, new host plants and habitats. This new finding increases the taxonomic diversity of the Grès à Voltzia fauna, expanding our knowledge of Early Triassic Aphidomorpha diversity and evolution.

Key words: Hemiptera, Aphidomorpha, fossil aphid, phylogeny, Triassic, Anisian, Vosges, France.

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Introduction

The early Aphidomorpha, like most of the Sternorrhyncha, are poorly known from the Triassic. *Triassoaphis cubitus* Evans, 1956 was reported from the Carnian deposits of Ipswich, Australia, and later assigned to a monogeneric family Triassoaphididae Heie, 1999 (Evans 1956; Heie 1981, 1999). The second known early aphidomorph, *Creaphis theodora* Shcherbakov and Wegierek, 1991, was described from the Ladinian–Carnian Dzhailou-Tcho (South Fergana, Kyrgyzstan), and placed in its own family Creaphididae Shcherbakov and Wegierek, 1991 (Shcherbakov and Wegierek 1991).

A supposed aphid fossil, *Dubiaphis curvata* Brauckmann and Schlüter, 1993, was also described from the Middle Anisian of former quarry at Herolds-Berg N'Hammelburg, Germany (Brauckmann and Schlüter 1993). However, this taxon's placement in the Aphidomorpha, and even in the Sternorrhyncha, remains dubious.

The superfamily Naibioidea Shcherbakov, 2007 was established to contain fossils from the Early Mesozoic of Kyrgyzstan, placed in the family Naibiidae Shcherbakov, 2007. This family comprises the subfamilies Coccavinae Shcherbakov, 2007 (*Coccavus* Shcherbakov, 2007 from the Middle Triassic of Madygen, Dzhailou-Tcho, Kyrgyzstan; and *Panirena* Shcherbakov, 2007, from the Middle Jurassic, Kubekovo, Siberia, Russia), and the Naibiinae Shcherbakov, 2007 (*Naibia* Shcherbakov, 2007 from the Palaeocene amber of Sakhalin Peninsula, Russia; Shcherbakov 2007, 2008b). Later, another family, the Sinojuraphididae Huang and Nel, 2008 from the Middle Jurassic, Daohugou, Inner Mongolia, China, was added to the Naibioidea (Huang and Nel 2008), followed by the family Dracaphididae Hong, Zhang, Guo and Heie, 2009, from the Ladinian of Shaanxi, China (Hong et al. 2009). The placement of Naibioidea within the Sternorrhyncha is still under discussion. Originally, Shcherbakov (2007) considered this superfamily to be "basal" to the Coccinea Beier, 1938 (his unit Coccomorpha). Hong et al. (2009) and Heie and Wegierek (2009a, b) both placed the Naibioidea within Aphidomorpha, arguing against some of the characters presented by Shcherbakov (2007).

The most recent proposal of aphidomorphan classification by Heie and Wegierek (2009a, b) presents the superfamily Triassoaphidoidea as containing two families: Triassoaphididae and Creaphididae. The superfamily is characterised by a long and slender pterostigma, long RP departing from the base or middle of pterostigma, three-branched M departing close to

the base of pterostigma, and CuA shaped as a fork with a moderately long stem.

Based on this diagnosis, the fossil described below belongs in this superfamily, but differs enough from the known Triassoaphidoidea families to merit new family status.

Institutional abbreviation.—EOST, Ecole Observatoire des Sciences de la Terre, Université Louis Pasteur, Strasbourg, France.

Other abbreviations.—Sc, subcosta; R, radius, M, media; CuA, cubitus anterior; Sc+R+(M)+CuA, common stem of veins subcosta, radius, media and cubitus anterior; $ScRA_1$, common branch of subcosta and first branch of radius anterior; RA, radius anterior; RA_2, second terminal of radius anterior; RP, radius posterior; M_{1+2}, common branch of media 1 and 2; M_{3+4}, common branch of media 3 and 4; M_1, first terminal of media; M_2, second terminal of media; CuA_1, first branch of cubitus anterior; CuA_2, second branch of cubitus anterior; A_1, first anal vein; Pcu, postcubitus, R1, first branch of radius.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Sternorrhyncha Amyot and Serville, 1843

Infraorder Aphidomorpha Becker-Migdisova and Aizenberg, 1962

Superfamily Triassoaphidoidea Heie, 1999

Family Vosegidae nov.

Type genus: Vosegus gen. nov.; designated herein.

Diagnosis (forewing).—Pterostigma well developed, elongate, with posterior margin arcuate (Creaphididae with pterostigma elongate with posterior margin straight, tapering apicad). Common stem Sc+R+(M)+CuA thick; RP arcuate, arising from Sc+R distinctly basad of pterostigma base, reaching margin well basad of wing apex (in Creaphididae RP curved only at base, arising from very base of stigma, reaching margin at apex of wing); M three-branched, with basal part not visible ("phantom" vein) and not distinctly touching common stem of Sc+R (in Creaphididae base of M curved at base, projecting to the point of CuA separation). Common stem of CuA about as long as common stem of M (in Creaphididae common stem CuA short, distinctly shorter than common stem of M); CuA as thick as M and RP (in Creaphididae CuA thicker than M and distal portion of R).

Genus *Vosegus* nov.

Etymology: derived from Vosegus—a Celtic god of hunting and forest from Eastern Gallia. Gender masculine.

Type species: *Vosegus triassicus* sp. nov.; designated herein.

Diagnosis (forewing).—Costal cell relatively wide. Pterostigma length ~3.7× width. RP arcuate, separated from common stem Sc+R at distance of costal cell width at base of

stigma. M stem distinctly shorter than M_{3+4}, M_{1+2} forked at level of stigma apex, M_{1+2} probably slightly shorter than terminal M_2. CuA stem ~0.5× as long as CuA_1 and about as long as CuA_2.

Vosegus triassicus sp. nov.

Fig. 1

Etymology: specific epithet derived from the Triassic period.

Type locality: Arzviller, department Moselle, Vosges, France.

Type stratum: Lower Anisian ("Upper Buntsandstein"), early Middle Triassic "Grès à Voltzia" Formation (Gall and Grauvogel-Stamm 2005).

Holotype: only single specimen known, forewing: EOST No. 5916 (part), 5917 (counterpart), Louis Grauvogel Collection, housed in EOST, Strasbourg, France.

Diagnosis.—As for genus.

Description.—Holotype forewing over 2.3 mm long (base and apex weakly preserved), and about 0.8 mm wide (length/width proportion may be slightly affected by distortion caused by preservation in matrix). Costal margin distinct, but not thickened. Costal cell slightly narrower than radial cell. Stem Sc+R+(M)+CuA very thick at base, straight, slightly curved at level of CuA stem separation; Sc forms deep furrow along R+M, weakened basad of CuA stem. Sc+RA_1 separated at level of M stem forking, forming basal border of stigma; RA_2 (R1 in interpretation of Shcherbakov 2007) slightly arcuate, delimiting posterior margin of stigma; RP ~0.9 mm long from base to apex ; RP separated well basad of stigma base, arcuate, reaching wing margin basad of apex. M stem 0.35 mm from base to apex, with sclerotised part 0.22 mm long; its base, if prolonged to stem, reaching it at shorter distance than CuA stem. M forked at level of pterostigma base; M_{1+2} about 0.5 mm long, distinctly shorter than terminal M_2, terminals M_1 and M_2 subequal in length (both ~0.3–0.5 mm), terminal M_{3+4} 0.66 mm long, slightly curved in apical portion. CuA stem 0.25 mm long, diverging at 50°, short, length roughly same as the distance between common stem and first forking of M stem, and shorter than terminal CuA_2 length; terminal CuA_1 about twice as long as terminal CuA_2 (0.75–0.8 mm and 0.3–0.4 mm long respectively). Claval furrow and Pcu+A_1 not preserved. Nodal flexion line not visible (if present).

Veins and pterostigma darkened (more sclerotised?), membrane unicoloured, probably hyaline.

Morphological characters of Triassic aphids and their relatives

The Permian Archescytinidae are considered to be ancestral to all extinct and Recent Hemiptera lineages (Shcherbakov and Popov 2002). In his discussion on the evolution of aphid morphological structures, Shaposhnikov (1980) stated that the homonomous wings of Archescytinidae (Paleorrhyncha) were converted to heteronomous wings of aphids. Later, Shcherbakov (2007) presented a list of characters, including
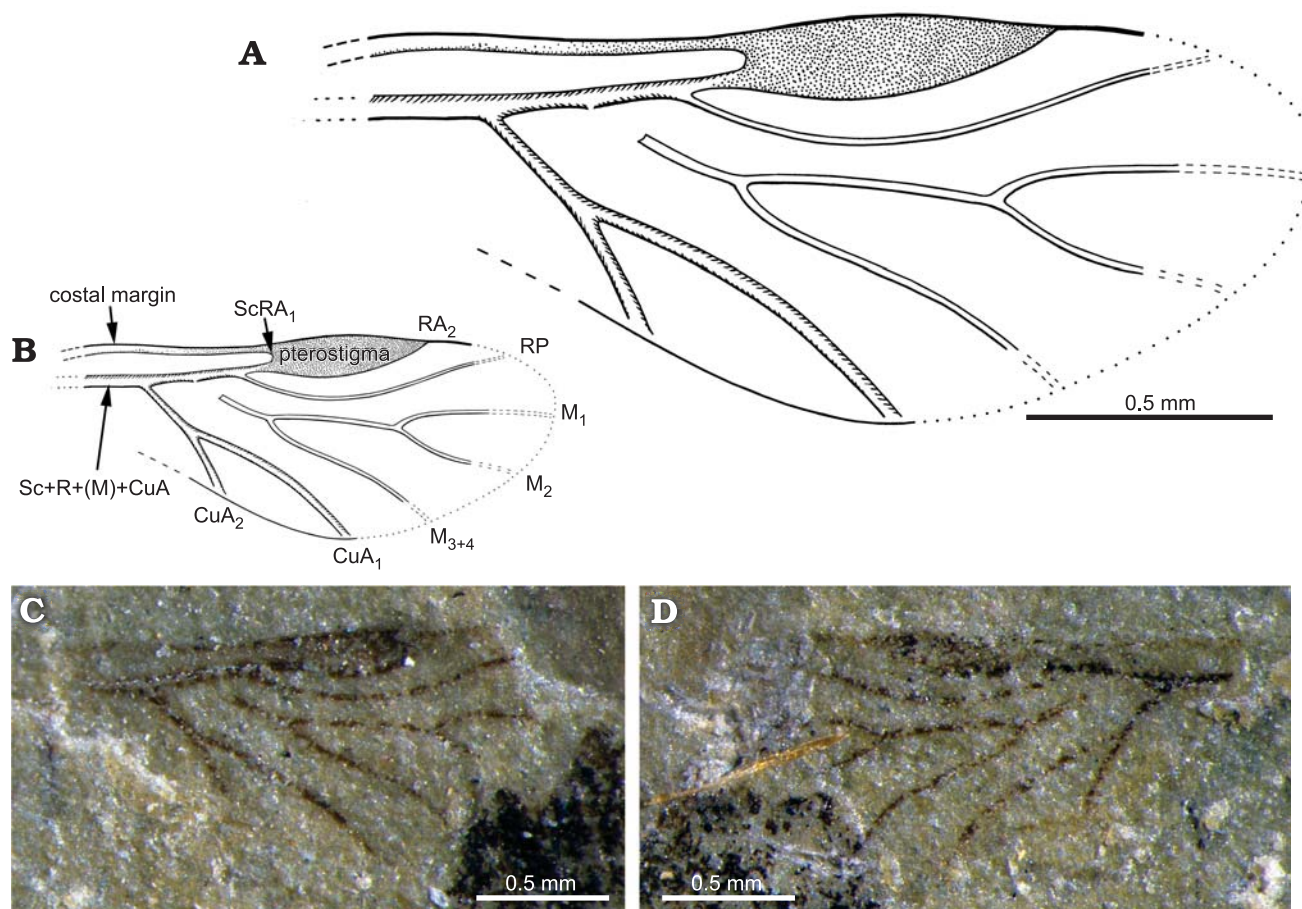
Fig. 1. Forewing of the early Middle Triassic (early Anisian) aphid *Vosegus triassicus* gen. et sp. nov. **A**. Reconstruction. **B**. Venation scheme. **C**. Part (No. 5916). **D**. Counterpart (No. 5917).

venation patterns, vein homology and forewing and hind wing transformations, for the Sternorrhyncha, including aphidomorphs. Shcherbakov (2007: 59) stated that although the extant Sternorrhyncha are diphyletic, the transition from Paleorrhyncha to Hemelytrata (= Euhemiptera) was not as gradual as those from Paleorrhyncha to Psylliformes and Pincombeomorpha (an extinct group related to the Aphidiformes, i.e., Aphidomorpha and Coccomorpha).

The opinion that the Sternorrhyncha are non-monophyletic is not universally accepted; indeed, there is strong support for sternorrhynchan monophyly, particularly from molecular data (Ouvrard et al. 2000; Gullan and Martin 2003; Grimaldi and Engel 2005; Forero 2008). Almost certainly, the Aphidomorpha constitute a monophyletic unit (Heie and Wegierek 2009a, b); with the progressive evolution of aphid wings interpretable as transformations partly specific to Aphidomorpha, occurring during the Permian-Triassic (Fig. 2), and partly shared with other insects (Fig. 3). It seems that these evolutionary changes are related less to the acquisition of new structures, than to the transformation, and frequently the loss, of old ones. The shape of aphid wings is modified from an elongated form with more or less parallel anterior and posterior margins (Archescytinidae), to a rounded, triangular shape. This was achieved by the narrowing of the anal region, and also the reduction of costal area (Shaposhnikov 1980).

The wing of *Vosegus* is similar in shape to *Creaphis*, clearly differing from the very elongated wing of *Triassoaphis*. The forewing structure of *Triassoaphis cubitus*, described by Evans (1956) and discussed and re-described by Heie (1967, 1981), remains poorly known. However, the length of the *Triassoaphis* forewing seems to be 3× width, whereas in *Creaphis* the ratio is about 2.7×, and in *Vosegus* it is about 2.5×. The costal margin in *Creaphis* is curved at base, but unfortunately this wing section is unclear in *Vosegus*. In *Creaphis,* the portion of costal margin at the pterostigma level is straight, but is instead slightly convex in *Vosegus*. This curvature could be related to the enlargement and shortening of pterostigma in *Vosegus* compared to *Creaphis* and *Triassoaphis*. The enlargement of the pterostigma follows the anterior concentration of veins, i.e. wing costalisation, and in turn could be correlated with a decrease in wing size, as this feature is observed among various Sternorrhyncha, and in unrelated Diptera and Hymenoptera (Rohdendorf 1946; Rasnitsyn 1969; Shaposhnikov 1980; Shcherbakov 2007).

The origin of RP (RS according to model proposed by Shcherbakov 2007), basad of the stigma's posterior margin
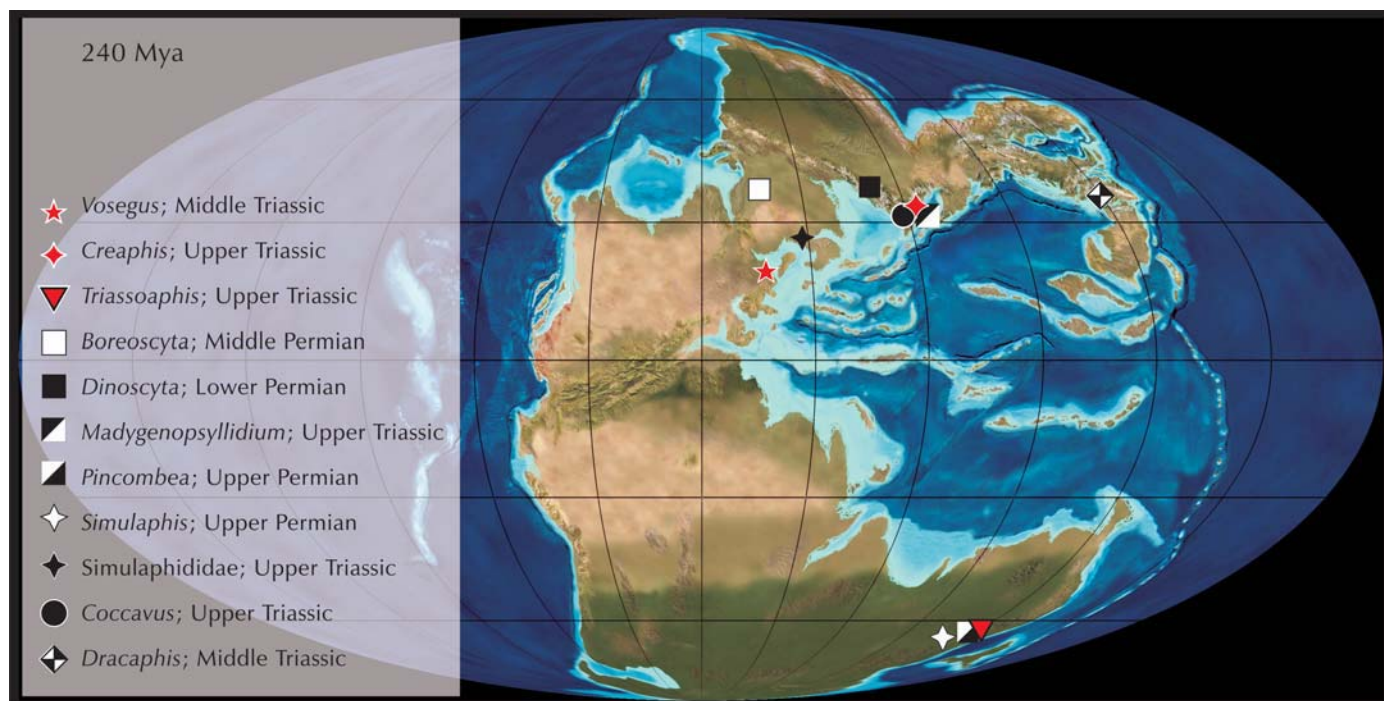
Fig. 2. Distribution of Permian and Triassic Aphidomorpha (Middle Triassic, 240 Ma). *Vosegus* (Aphidomorpha: Triassoaphidoidea: Vosegidae); Middle Triassic, Anisian; "Grès à Voltzia" Formation, France; *Creaphis* (Aphidomorpha: Triassoaphidoidea: Creaphidae); Upper Triassic, Carnian; Dzhailou-Tcho, Madygen Formation, Kyrgyzstan; *Triassoaphis* (Aphidomorpha: Triassoaphidoidea: Triassoaphididae); Upper Triassic, Carnian; Belmont, NSW, Australia; *Boreoscyta* (Pincombeomorpha: Pincombeoidea: Boreoscytidae); Upper Permian, Roadian; Soyana, Russia; *Dinoscyta* (Pincombeomorpha: Pincombeoidea: Boreoscytidae); Lower Permian, Kungurian; Koshelevka Formation, Chekarda, Russia; *Madygenopsyllidium* (Pincombeomorpha: Pincombeoidea: Pincombeidae); Upper Triassic, Carnian; Dzhailou-Tcho, Madygen Formation, Kyrgyzstan; *Pincombea* (Pincombeomorpha: Pincombeoidea: Pincombeidae); Upper Permian, Lopingian (Changhsingian); Newcastle Coal Measures, NSW, Australia; *Simulaphis* (Aphidomorpha: Naibioidea: Simulaphididae); Upper Permian, Lopingian (Changhsingian); Newcastle Coal Measures, NSW, Australia; Simulaphididae indet. (Aphidomorpha: Naibioidea); Upper Triassic, Carnian; Garazhovka Formation, Ukraine; *Coccavus* (Aphidomorpha: Naibioidea: Naibiidae); Upper Triassic, Carnian; Dzhailou-Tcho, Madygen Formation, Kyrgyzstan; *Dracaphis* (Aphidomorpha: Naibioidea: Dracaphididae); Middle Triassic, Ladinian; Tongchuan Formation, Shaanxi, China.

(i.e., Sc+RA$_1$) in *Vosegus*, is a feature also shared by *Simulaphis* Shcherbakov, 2007 (Pincombeomorpha) and *Archescytina* Tillyard, 1926 (Archescytinidae), and probably is a plesiomorphic state. In this respect, *Vosegus* presents a more basal condition for this feature than *Creaphis*, in which RP originates at the level of the pterostigma posterior margin, and other aphids where this apicad shifting is more strongly developed, such as the Jurassic genera *Genaphis* Handlirsch, 1907, *Juraphis* Shaposhnikov, 1979, and *Jurocallis* Shaposhnikov, 1979 (Shaposhnikov 1979). A very long RP, which leaves the long, slender and pointed pterostigma not far from its base, is also seen in many extinct genera as *Sinojuraphis*, *Triassoaphis*, and *Nordaphis*, and can be found among extant subfamilies of the Drepanosiphidae, namely Mindarinae (M with two branches), Neophyllaphidinae (M with three branches) and Lizeriinae (M with two or three branches). The Drepanosiphidae causes a number of problems in sternorrhynchan classification and phylogeny, even though most of its characters appear to be plesiomorphies (Heie and Wegierek 2009a, b). However, in the most recent proposal (Heie and Wegierek 2009a, b), Drepanosiphidae were considered a monophyletic unit containing a number of subunits previously considered separate.

In *Vosegus*, the common portion of M is transformed into a light concave fold, probably allowing easier changes in the wing camber during the upstroke, as suggested by Shcherbakov (2007). The phantom-like basal portion of M, which is not adjoined to the Sc+R stem, is a feature also present among the Palaeoaphididae, Ellinaphididae, Genaphididae, and Canadaphididae. A three-branched M can be observed among various aphids from the Triassic (*Triassoaphis*, *Creaphis*, *Vosegus*), Jurassic (Genaphididae: *Genaphis* Brodie, 1845), and Cretaceous (Palaeoaphidoidea: Ellinaphididae, Szelegiewicziidae and some Shaposhnikoviidae; Genaphidoidea: Genaphididae, e.g., *Tinaphis* Wegierek, 1989; and Aphidoidea: Oviparosiphidae, Canadaphididae, Sinaphiumidae). A two-forked media is suggested to be the ancestral condition for all aphidomorph subfamilies, and is also present in other paraneopteran groups (basal Thripida and Psocodea; Heie 1981; Heie and Wegierek 2009a, b).

CuA with a basal stem and a distal fork, as observed in the Triassic Aphidomorpha (*Creaphis*, *Triassoaphis*, and *Vosegus*), is also retained in the Jurassic *Genaphis* Becker-Migdisova, 1966 and *Juraphis* Shaposhnikov, 1971. The presence of the basal stem of CuA is a plesiomorphic character, which can be observed in both the ancestors of aphids and basal
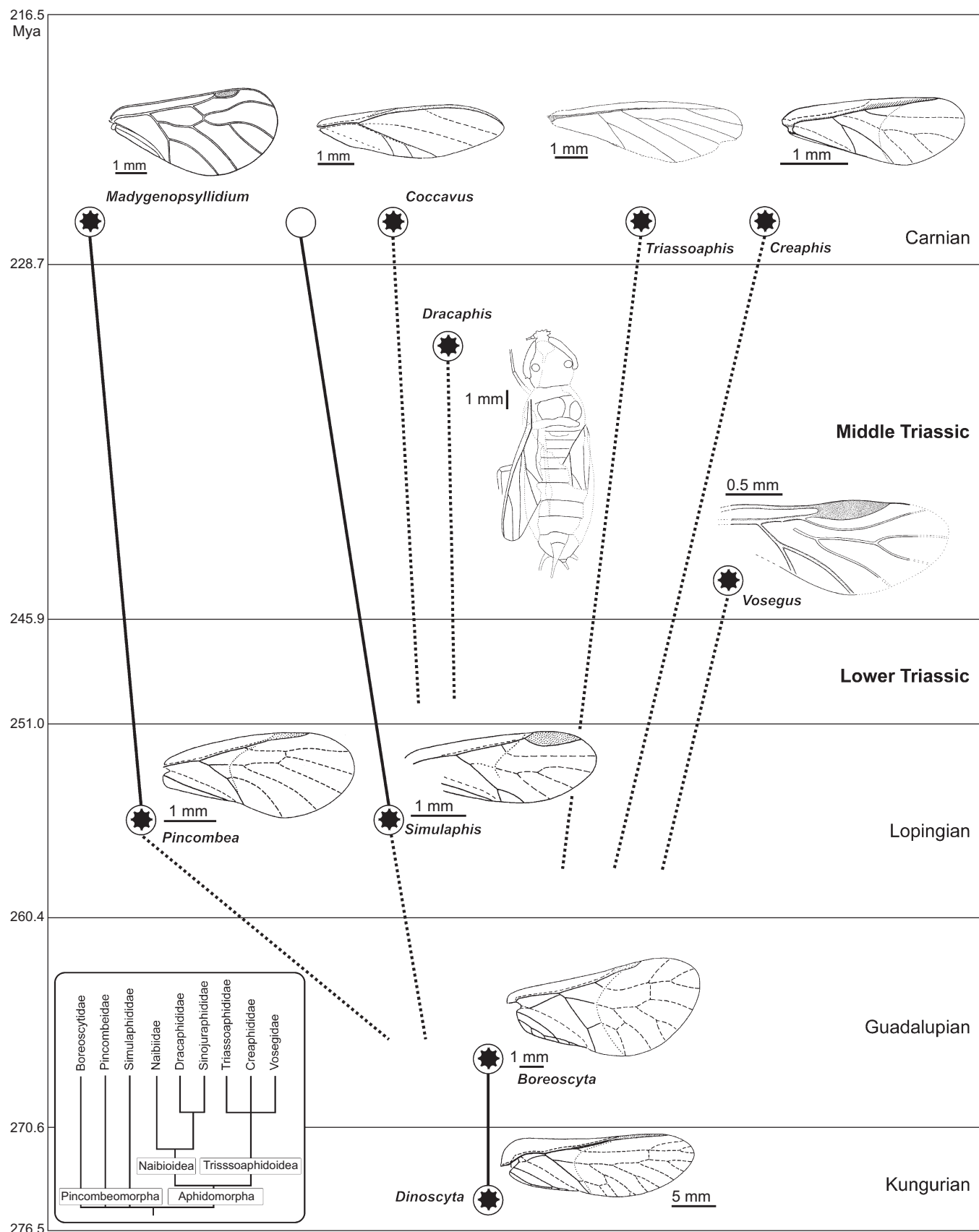
Fig. 3. Schema of range and relationships of Permian and Triassic Aphidomorpha and their relatives. Asterisks in circle, mean taxa figured in the schema; empty circle, non figured taxon. Insert: supposed cladogram of Permian and Triassic Aphidomorpha, inferred from data and opinions from Shcherbakov (2007) and Heie and Wegierek (2009a, b).

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Paraneoptera (Shcherbakov 1990, 2007). In the Recent Aphidomorpha, a distinct basal branch of CuA with a distal fork can be found in some representatives of the family Phylloxeridae (Phylloxeroidea), Hormaphididae, and exceptionally, in Eriosomatidae (Aphidoidea). Nevertheless, in these families M is usually single, not forked. In *Vosegus*, the branches of CuA are not thickened, a state found in most of the Aphidomorpha, apart from the Elektraphididae (Adelgoidea).

The claval portion of *Vosegus* is not preserved, although by extrapolation of the general shape of wing and by analogy with other Triassic aphids, it is estimated to be narrow. In *Creaphis*, the claval furrow is distinct, slender, and almost reaches the CuA_2 apex. The claval veins $Pcu+A_1$ border the clavus posteriorly in this genus, continuing across the CuA_2 apex as a coupling fold (Shcherbakov and Wegierek 1991). Such an arrangement is also very probable for *Vosegus*, as Shcherbakov and Wegierek (1991) stated that a slight and hardly perceptible (i.e., nonfunctional) claval furrow and convex marginal $Pcu+A_1$ are nearly universal amongst the Aphidomorpha.

Although the characters mentioned above are spread among the different extinct and extant lineages of Aphidomorpha, the combination presented by *Vosegus* is unique among the known representatives of this group.

The known Triassic forms (*Creaphis*, *Triassoaphis*, and *Vosegus*), all based on isolated fossil wings, may represent the basal group of both the Coccinea sensu lato and other aphids (see discussion in Shcherbakov 2007; Huang and Nel 2008; Hong et al. 2009; Heie and Wegierek 2009a, b). The Dracaphididae from the Middle Triassic of China are very similar to the Sinojuraphididae in body features (Huang and Nel 2008; Zhang and Hong 2009; Hong et al. 2009), and it was suggested that the three lineages leading to extant aphids, i.e., Adelgoidea, Phylloxeroidea, and Aphidoidea (with the other extinct aphid superfamilies), were separated in the Triassic–Jurassic (Wojciechowski 1992; Heie and Pike 1992, 1996; Heie 1996; Wegierek 2002). Hong et al. (2009) instead considered the Naibioidea to be the sister group to all other aphids, except perhaps the earlier separated Phylloxeroidea and Adelgoidea, and that they diverged in the Triassic, or even as early as the Permian. This statement was also supported by Heie and Wegierek (2009a, b), who suggested that the Phylloxeroidea separated first, and Adelgoidea also separated before the clade containing Naibiidae + Sinojuraphididae split from the other recognised extinct superfamilies of Aphidomorpha. In this view, Naibioidea, together with all other extinct aphidomorph superfamilies—(Triassoaphidoidea + (Genaphidoidea + Palaeoaphidoidea + Tajmyraphidoidea))—forms a sister group to clade clade (Aphidoidea + (Adelgoidea + Phylloxeroidea)) (Heie and Wegierek 2009a).

The general pattern of aphidomorph evolution is very difficult to resolve. As suggested by Heie and Wegierek (2009a, b), a single "character" can show up at any time during evolution and disappear again, making the general picture more like a puzzle or mosaic than a tree. It is possible that some genes are always present, but become dormant during certain periods.

Palaeoenvironmental changes and early stages of aphid evolution

One of the most important climatic and biological crises in Earth history took place 250 Mya ago during the Permian to Triassic transition. The end-Permian mass extinction is now robustly dated at 252.6 ± 0.2 Mya (U–Pb), with the Permian–Triassic (P–T) GSSP level dated by interpolation at 252.5 Mya (Metcalfe and Isozaki 2009). At the end of the Permian, 85–95% of marine and land species disappeared and the life forms that characterised the Mesozoic and the Cainozoic began to develop. Recently various aspects of this biotic crisis, and associated Early Triassic biotic recovery have been presented, analysed, and discussed (Zharkov and Chumakov 2001; Chumakov and Zharkov 2003; Béthoux et al. 2005; Bottjer and Gall 2005; Grauvolgel-Stamm and Ash 2005; Ponomarenko 2006; Shcherbakov 2008a; Virgili 2008). With the start of the Mesozoic in the Triassic, the world we know today started to take the shape. Pangea started to break up, heralding an important palaeogeographical change. The Pangean supercontinent typifies Permian and Triassic geography (Fig. 2), migrating 25° northward through these intervals, so that in the Early Permian the north and south polar regions were ocean and land, respectively, but the opposite was true by the Late Triassic. A number of microcontinents (e.g., North and South China) traversed low latitudes during the Permian, but most of these had collided with the main Pangean landmass by the Late Triassic (Rees et al. 2002). The Late Permian–initial Triassic was also a period of global climate change, as the glacial climate of the Late Palaeozoic was replaced by the non-glacial Mesozoic (Chumakov and Zharkov 2003). The vast area of the Pangean supercontinent, as well as its north-south orientation, stretching nearly from pole to pole, had a profound effect on terrestrial climates during the period, which was characterised by strong seasonality, and was likely quite dry. Global warming, due to increased levels of CO_2 in the atmosphere, resulted in an expansion of arid climates into high latitudes in the Northern Hemisphere, and the shift of deciduous forests towards the Southern Hemisphere's polar regions. Atmospheric circulation system changed and CO_2 levels underwent a substantial increase during the Permian–Triassic interval, remaining high throughout the Triassic, and atmospheric O_2 levels decreased during the Early Triassic (Zharkov and Chumakov 2001; Chumakov and Zharkov 2003; Grauvogel-Stamm and Ash 2005; Woods 2005).

As land plants are very sensitive to climatic change (Grauvogel-Stamm and Ash 2005), significant floral changes occurred during the Triassic, resulting in three floral stages: the first stage lasted from the Induan to Anisian; the second occurred in Ladinian and Carnian; and the third was in the

Norian and Rhaetian (Dobruskina 1988a). Flora from the lower part of the Triassic was palaeophytic, characteristic of expansion of *Pleuromeya* flora (Dobruskina 1988a, b); however, mesophytic floral elements were also present in the late Early Triassic (Rothwell et al. 2000). The Early Triassic peculiarity is reflected both in the composition and distribution of the fossil floras, and differs from the Palaeozoic (which shows a degree of isolation and differentiation of the phytochoria) and Mesozoic (characterised by the homogeneity of its floras) in the vast expansion of lycopods through all the phytochoria. The western European and Chinese floras with their xeromorphic plants belonged to the united European–Sinian palaeofloristic area that was once part of the Laurasian kingdom (Dobruskina 1988b). In Europe, the Early Triassic landplant recovery went through two stages: a survival interval dominated by the lycopsid *Pleuromeya* Corda ex Giebel, 1853 (= *Pleuromeia*: Stiechler 1859); and a recovery interval characterised by the resurgence of gymnosperms.

The Grès à Voltzia Formation of eastern France, in which *Vosegus* was found, has a flora dominated by various conifers, e.g., *Voltzia* Brongniart, 1828, *Albertia* Schimper in Voltz, 1837, *Aethophylum* Brongniart, 1828, and *Pelourdea* Seward, 1917 (= *Yuccites* Schimper and Mougeot, 1844 non Martius, 1822) (Grauvogel-Stamm and Ash 2005). Among the plants found there are two lycopsids, five sphenopsids, three ferns, one cycad, one ginkgophyte, and 15 different conifers; however, the association from this site shows many similarities with the Permian flora (Gall and Grauvogel-Stamm 2005). The dominant plant recovered from "Grès à Voltzia", *Aethophyllum stipulare* Brongniart, 1828 (Voltziales), was an herbaceous plant of only one or two meters high, whereas most fossil and Recent conifers are shrubby or arborescent. Moreover, in very poor environmental conditions, the height of *Aethophyllum* was likely even more reduced. This conifer is interpreted as a fast-growing, opportunistic species, rapidly invading vacant ecospaces thanks to the prolific production of small seeds (Grauvogel-Stamm 1978; Taylor et al. 2009). Size reduction has been documented in the flora of "Grès à Voltzia", particularly for *Aethophyllum*. It is suggested that the host plant of the Vosegidae were conifers, and most likely the common *Aethophyllum*.

Evidence from sedimentary structures and palaeoecological data indicate that "Grès à Voltzia" was a deltaic environment, likely a patchwork of small habitats harbouring low diversity communities including Palaeozoic survivors, Lazarus taxa and "modern" genera, an association not yet described anywhere else in the world (Gall and Grauvogel-Stamm 2005).

The rich entomofauna of the "Grès à Voltzia" needs more extensive investigation, as its systematics remains unsatisfactory at the family level. Gall and Grauvogel-Stamm (2005) suggested that only a part of the fauna is described so far, yet representatives of 12 orders have been recognised: nine species of Ephemeroptera, two species of Odonatoptera, one undetermined Plecoptera, four species of Orthoptera, five described Blattodea (most abundant fossils), one species of Phasmatodea, three described species of Hemiptera (but likely higher in diversity), several undetermined Neuroptera, three species of "Mecoptera", one species of Trichoptera, seven species of Diptera (described after adults, but many larvae and pupae are also recorded; Lukashevich et al. 2010), and about 30 species of Coleoptera.

The vast majority of insects from the "Grès à Voltzia" locality are represented by isolated wings, the size of which varies from 2 to 20 mm, with an average of 5–6 mm (Gall and Grauvogel-Stamm 2005). This reduction in size has been correlated with the refugial character of the "Grès à Voltzia" environment, and therefore the "Lilliput effect" (Grauvogel-Stamm and Ash 2005; Gall and Grauvogel-Stamm 2005). The "Lilliput effect" was named by Urbanek (1993) in his study on the recovery of graptoloids after the Silurian biotic crisis, and is a phenotypic response to unfavourable conditions prevailing immediately after this biotic crisis. A different interpretation of the body size reduction seen during this Silurian event has been suggested by Twitchett (2001): the drop of primary productivity during the crisis involves a decrease in the biomass, which leads to a reduction either in abundance of the populations, or in body size of the taxa. It has been hypothesised that marginal environments, such as those in "Grès à Voltzia", may have acted as refugia during these various life crises, i.e., as habitable areas in an otherwise inhospitable world (Grauvogel-Stamm and Ash 2005; Gall and Grauvogel Stamm 2005).

These ideas seem to be disputable for Grès des Vosges because it is several million years after the end-Permian crisis. However, it is the first rich and diverse outcrop known after the crisis, and the pattern may simply be due to random effects and/or a lack of investigation. The question is also arising: does the fossil record of Permian insects allow for very small insects? In many Permian outcrops, small insects are rare due to taphonomic bias. Forewings of Pincombeomorpha Shcherbakov, 1990, the supposed Permian ancestors of Aphidomorpha, are relatively large: *Boreoscyta* Becker-Migdisova, 1949 from Middle Permian of Northern Russia has forewings 5.6–9 mm long, whereas forewings of *Dinoscyta* Shcherbakov, 2007 from Lower Permian of Urals were 12–23 mm long (Shcherbakov 2007). In the Upper Permian, *Pincombea* Tillyard, 1922 forewings are 3.1–4.7 mm, and in the Middle (Upper) Triassic, *Madygenopsyllidium* Becker-Migdisova, 1985 forewings were slightly bigger at 5.4 mm long (Becker-Migdisova 1985). Diminution of size in comparison to some (but not all) Pincombeomorpha is also observed in the Simulaphididae Shcherbakov, 2007—the tegmen of *Simulaphis* Shcherbakov, 2007 from the Upper Triassic of Belmont, NSW, Australia, is about 3.5 mm long. Middle and Upper Triassic Naibioidea are also rather small forms, but still bigger than *Vosegus*—e.g., *Coccavus* Shcherbakov, 2007 from Middle (Upper) Triassic of Madygen in Kyrgyzstan has a tegmen 4.5 mm long; the forewing of *Dracaphis* Hong, Zhang, Guo, and Heie, 2009 from the Middle Triassic of Shaanxi, China is 5.2 mm long (Fig. 3). Interestingly, Vosegidae and Creaphididae (the latter being slightly younger than *Vosegus*) are simi-

lar in size, whereas the Late Triassic Triassoaphididae were distinctly bigger, with a tegmen length about 6 mm (Evans 1956; Heie 1981). Therefore, the "Lilliput effect" could not be the only explanation for the size variability in Aphidomorpha. An alternative solution to this question could be that aphids diversified into a special niche, correlated to their small size, allowing them to feed on particular plant parts not exploited by other insects. In discussing some synapomorphies of Aphidomorpha in respect to other related groups, Shcherbakov (2007) stated that the Aphidomorpha + Coccomorpha evolved towards the diminution of the body size and costalisation of coupled wings, and therefore to the reduction of the clavus and hindwing, leading to subdiptery and true diptery in male coccids. Shcherbakov (1990, 2000) indicated conifers as the host plants for several primitive groups of Aphidomorpha, particularly the lineage descending from archescytinids via Pincombeidae and Boreoscytidae (Pincombeomorpha). Permian Archescytinidae probably laid eggs into the gymnosperm female cupules and strobili (Becker-Migdisova 1985), where their flattened nymphs dwelt until the seeds ripened; early aphid diversification may therefore be correlated to the exploitation of new niches, rather than from the low productivity of its host plant or unfavourable (patchy?) habitat conditions (warming and drying, high seasonality?). Therefore, the decrease of size in Aphidomorpha may parallel a similar phenomenon in Thripida during the Mesozoic (Nel et al. in press), and which may have occurred for similar reasons, even if insects of the thysanopteran lineage are more likely to feed on spore and pollen.

Note added in proof

After the formal acceptance of our paper by *Acta Paleontologica Polonica* (27 December 2010), we were informed by Dmitri E. Shcherbakov (19 March 2011) that the specimen being base of our description was already published by him in *Russian Entomological Journal* (in November 2010 according to the journal frontispiece; September 2010 is given on title page). Therefore the names proposed by us are junior synonyms of those proposed by Shcherbakov (2010). They are as follows:

Leaphidinae Shcherbakov, 2010: 180.
= Vosegidae Szwedo and Nel, 2011: 758.
Leaphis Shcherbakov, 2010: 180.
= *Vosegus* Szwedo and Nel, 2011: 758.
Leaphis prima Shcherbakov, 2010: 180, figs. 6–7.
= *Vosegus triassicus* Szwedo and Nel, 2011: 758.

Shcherbakov (2010) described subfamily Leaphidinae in the family Creaphididae Shcherbakov and Wegierek, 1991. In the same paper he suppressed the superfamily Triassophidoidea under Paleoaphidoidea, but gave no arguments for this action or opinion on content of this superfamily. Shcherbakov (2010) is not referring to the most recent classification and definitions of families and superfamilies proposed by Heie and Wegierek (2009a, b).

Triassophidoidea comprises families Triassophididae and Creaphididae according to Heie and Wegierek (2009a, b). According to them, Triassoaphididae are characterized as follows: only a fore wing is known; wing veins very long; radial sector straight, nearly reaching pterostigma, leaving middle of it; media departing from base of pterostigma; and family Creaphididae as follows: only a fore wing is known; pterostigma reaching wing apex; subcosta forming a deep furrow along radius and media; radial sector very long, leaving base of pterostigma; CuA$_1$ thicker than media and distal part of radial sector (Heie and Wegierek 2009b). Palaeoaphidoidea comprised families Palaeoaphididae Richards, 1966, Ellinaphididae Kania and Wegierek, 2008, Szelegiewicziidae Wegierek, 1989, and Shaposhnikoviidae Kononova, 1976 and were given following description: only alatae known; fore wings often strongly narrow in basal part; media with one or two forks; cubitus shaped as a fork or its branches separated at bases; hind wings with tendency to shortening; antennae 5- to 7-segmented; siphunculi absent; oviparous (Heie and Wegierek 2009b).

According to diagnosis of Shcherbakov (2010), Creaphididae are characterized by: pterostigma elongate to linear, not reaching wing apex; RP separating near base of pterostigma or from its distal part; M with three branches; distal part of M stem projecting onto Sc+R far from CuA base; CuA stem shorter than CuA$_2$; claval furrow and claval vein developed and comprises three subfamilies: Triassoaphidinae, Creaphidinae, and Lepahidinae.

In our opinion the actions of Shcherbakov (2010) are premature and we propose to sustain Triassoaphidoidea as a superfamily with three families: Triassoaphididae, Creaphididae, and Leaphididae stat. nov. His opinion on the similar range of morphological disparity in *Creaphis* Shcherbakov and Wegierek, 1991 and *Leaphis* in comparison with the disparity observed among polyphyletic and highly variable Drepanosiphidae Herrich-Schaeffer, 1857 could be challenged, as most of drepanosiphid characters are apparently plesiomorphies (Heie and Wegierek 2009a). Difference in relative length of CuA stem in *Creaphis* and *Leaphis* also pointed as paralleled by the variation observed in Ellinaphididae is, however, used as diagnostic feature in this group (Kania and Wegierek 2008).

Shcherbakov (2010: 179) suggested also suppression of Dracaphididae Hong, Zhang, Guo, and Heie, 2009 under Naibiidae Shcherbakov, 2007, stating however that "... systematic affinities of these forms will be discussed separately." However, Heie and Wegierek (2009a, b) placed Naibioidea (as superfamily with families Naibiidae, Sinojuraphidiae Huang and Nel, 2008 and Dracaphididae) in Aphidomorpha.

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