How Time Flies for Flies: Diverse Diptera from the Triassic of Virginia and Early Radiation of the Order

VLADIMIR BLAGODEROV,[1] DAVID A. GRIMALDI,[2] AND
NICHOLAS C. FRASER[3]

ABSTRACT

The most diverse and best-preserved early fauna of flies (order Diptera) is described from the Late Carnian (Late Triassic, ca. 220 Ma) of Virginia, USA. Complete flies are preserved as aluminosilicate films on very fine-grained shales from the Cow Branch Formation, which is part of the Newark Supergroup of Early Mesozoic rift basins from eastern North America. The dipteran fauna consists of eight families (one new), 11 genera (five new), and 16 species (11 new), and includes the following taxa (Blagoderov and Grimaldi are the authors of all new names): *Architipula youngi* Krzemiński, *Metarchilimonia krzeminskorum* n.gen., n.sp., and *M. solita* n.sp. (Limoniidae); *Triassopsychoda olseni* n.gen., n.sp. (Psychodidae); Culicomorpha indet.; *Yalea argentata* (Krzemiński), *Y. rectimedia* n.sp., *Alinka cara* Krzemiński (Procramptonomyiidae); *Veriplecia rugosa* n.sp., *Virginiptera certa* n.gen., n.sp., *V. similis* n.sp., *V. lativentra* n.sp. (Paraxymyiidae); *Brachyrhyphus distortus* n.gen. n.sp. (Protorhyphidae); ?*Crosaphis virginiensis* n.sp. (Crosaphididae); and *Prosechamyia trimedia* n.gen., n.sp., *P. dimedia* n.sp. (Prosechamyiidae, new family). Particularly significant is a culicomorphan with a long proboscis, which is the earliest fossil record of a structure specialized apparently for blood feeding. Also, *Prosechamyia* appears to be a stem group to the very diverse infraorder Brachycera, the earliest definitive members of which appear in the Early Jurassic. Phylogenetic relationships of major clades of living and extinct nematocerous Diptera are analyzed, indicating that infraordinal-level diversification was complete by the Late Triassic. Flies did not reach modern levels of ecological abundance until the mid-Jurassic, apparently due to diversification within most infraorders by that time.

[1] Division of Invertebrate Zoology (Entomology), American Museum of Natural History; presently: Department of Entomology, The Natural History Museum, Cromwell Road, London UK.
[2] Division of Invertebrate Zoology (Entomology), American Museum of Natural History (grimaldi@amnh.org).
[3] Virginia Museum of Natural History, 1001 Douglas Avenue, Martinsville, VA 24112 (nfraser@vmnh.net).

INTRODUCTION

The Diptera, or true flies, comprise one of the oldest lineages of holometabolous insects, with the earliest definitive flies known from the mid-Triassic of France, approximately 230 Ma (Krzemiński and Krzemińska, 2003; Krzemiński et al., 1994). Since the Triassic, flies have evolved into one of the most diverse orders of living insects, with approximately 120,000 described species, and estimates place the actual numbers near one million or more (Gaston, 1991). Ecologically, flies are arguably the most diverse of all orders of insects, including species that are vertebrate ectoparasites, arthropod parasitoids, phytophages, pollenivores, predators, and, of course, saprophages (Grimaldi and Engel, 2005). In this study we make a substantial contribution to knowledge of the evolutionary history of the Diptera by describing the most diverse diperan fauna now known from the Triassic.

Relationships among the major clades, or infraorders, of Diptera is not settled (Hennig, 1973; Oosterbroek and Courtney, 1995; Wood and Borkent, 1989), which is due in part to vague concepts for some of the infraorders, such as Psychodomorpha and Bibionomorpha. Vague infraordinal concepts themselves may be a result of morphological work that is insufficient to date or in its entirety. This is doubtful, though, since the basal relationships of all other major holometabolous orders have been well resolved using morphological characters (Grimaldi and Engel, 2005), and there is no reason to believe Diptera should be any different. Unlike the other holometabolous orders, though, basal relationships of Diptera have not been examined using DNA sequences. If indeed the morphology of Recent Diptera is insufficient to resolve basal relationships, it is possible that early fossils could possess intermediate features that better reveal homologies, such as is the case with Tanyderidae and Psychodidae (Ansorge, 1994) and Valeseguyidae and Scatopsoidea (Amorim and Grimaldi, 2006). In taxa with extensive extinction of stem groups, obscure relationships among crown groups would be expected. Alternatively, relationships among crown groups can also be obscured if they diverged very close in time or simultaneously.

EARLY FOSSIL RECORD: The earliest and closest known relatives of flies appeared in the Permian. These include *Permotipula particia* Tillyard, 1929 and *Robinjohnia tillyardi* Martynova, 1948, from the Late Permian (Tatarian: 255 Ma) of Belmont and Warner's Bay, New South Wales, Australia (Willmann 1989a, b; Shcherbakov et al., 1995). Also related to Diptera, but more distantly, are the extinct families Liassophilidae (Triassic to mid-Jurassic of Eurasia) and the Permotanyderidae (Permian of Australia). *Permotipula* is known only from a single wing; specimens of the other groups were four-winged insects, though the hind wings of Liassophilidae were reduced in size. Deposits of insects from the Early Triassic are very rare (reviewed in Rasnitsyn and Quicke, 2002), and so there are no Diptera known from this period. In the mid- to Late Triassic, though, some 230–210 Ma, a sudden diversity of true (i.e., two-winged) Diptera occurred, representing all but one of the six living infraorders, 14 families (all but one extinct), and 28 species, not including the present study (table 1). Triassic Diptera are known from seven deposits in Asia, Australia, Europe, and North America (reviewed by Krzemiński 1992; Krzemiński and Evenhuis, 2000; Krzemiński and Krzemińska, 2003; Shcherbakov et al., 1995, fig. 4).[4] To date, no Diptera are known from the insect-bearing Triassic deposits in Argentina (Martins-Neto, 2003), and only one is known from the prolific Molteno Formation of South Africa (Anderson and Anderson, 1993), which is of indeterminate identity (Blagoderov and Grimaldi, unpubl.).

THE VIRGINIA TRIASSIC: All of the Diptera specimens based on the current study are from the quarries of the Solite Corporation in Cascade, Virginia (hereafter, the "Solite quarries") on the border of Virginia and North Carolina. These quarries lie in the Danville–

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[4]*Triassochoristites jinsuoguanensis* (Hong and Guo 2003) was recently described in the Mesopanorpodidae (Mecopterida) but probably belongs to the dipteran family Vladipteridae. This conclusion is based on the structure of the cubital complex, with a convex CuA and associated concave *iCu* vein, a distinct kink at the base of the radius, three long (R_3–R_5) veins and a short, oblique vein R_2 in the radial sector (this last vein was misinterpreted on the drawing, but is clearly seen on the published photograph). These are all apomorphies of Diptera.

TABLE 1

Described and Mentioned Triassic Diptera (species in boldface are described in this paper)

INFRAORDER TIPULOMORPHA			
Family Vladipteridae			
Vladiptera kovalevi Shcherbakov, 1995	Upper Tolgoi Formation	Kendyrlik, Kazakhstan Central Asia	Norian-Rhaetian
Dilemmala specula Shcherbakov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Psychotipa predicta Shcherbakov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Psychotipa depicta Shcherbakov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Triassochoristites jinsuoguanensis Hong et Guo, 2003	Tongchuan Formation	Tongchuan, Saanxi, China	Middle Triassic
Family Limoniidae			
Subfamily Archilimoniinae			
Archilimonia vegesiana Krzemiński, 2003	Grés a Voltzia	Vosges, France	Anisian
Subfamily Architipulinae			
Architipula youngi Krzemiński, 1992	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Mabelysia charlesi Shcherbakov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Metarchilimonia krzeminskorum, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Metarchilimonia solita, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Subfamily Gnomuscinae			
Gnomusca molecula Shcherbakov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Gnomusca renyxa Shcherbakov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
INFRAORDER PSYCHODOMORPHA			
Family Grauvogeliidae			
Grauvogelia arzvilleriana Krzemiński et al., 1994	Grés a Voltzia	Vosges, France	Anisian
Louisia nova Krzemiński, 2003	Grés a Voltzia	Vosges, France	Anisian
Family Nadipteridae			
Nadiptera kaluginae Lukashevich, 1995	Koldzat Formation	Ketmen', Kazakhstan, Central Aisa	Ladinian-Carnian
Nadiptera pulchella Lukashevich, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Tanus triassicus Krzemiński, 2003	Grés a Voltzia	Vosges, France	Anisian
Family Hennigmatidae			
Kuperwoodia benefica Lukashevich, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Anemea liya Shcherbakov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Family Tillyardipteridae			
Tillyardiptera prima Lukashevich et Shcherbakov, 1999	Lower Ipswich Series	Mt.Crosby, Queensland, Australia	Carnian
Family Rhaetaniidae			
Rhaetania dianae Krzemiński et Krzemińska, 2002	Lias Group	Stransham, UK	Rhaetian
Family Psychodidae			
Triassopsychoda olseni n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Family Eoptychopteridae			
Indet.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian

TABLE 1
(Continued)

INFRAORDER CULICOMORPHA
Family Chironomidae

Aenne triassica Krzemiński et Jarzembowski, 1999	Lias Group	Stransham, UK	Rhaetian
Family indet.			
Indet. sp. 1, 2	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
INFRAORDER BIBIONOMORPHA			
Family Procramptonomyiidae			
Yalea argentata (Krzemiński) 1992	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Yalea rectimedia, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Alinka cara **Krzemiński, 1992**	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Austrocramptonomyia minuta Blagoderov, 1999	Lower Ipswich Series	Mt.Crosby, Queensland, Australia	Carnian
Family Protorhyphidae			
Vymrhyphus tuomikoskii Blagoderov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Vymrhyphus triassicus Blagoderov, 1995	Madygen Formation	Dzhailoucho, Kyrgyzstan, Central Asia	Ladinian-Carnian
Vymrhyphus blagoderovi Krzemiński, 2003	Grés a Voltzia	Vosges, France	Anisian
Brachyrhyphus distortus, **n.sp.**	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Family Paraxymyiidae			
Veriplecia handlirschi Blagoderov, 1999	Lower Ipswich Series	Mt.Crosby, Queensland, Australia	Carnian
Veriplecia rugosa, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Virginiptera certa, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Virginiptera similis, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Virginiptera lativentra, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Family Crosaphididae			
Crosaphis anomala Evans, 1971	Lower Ipswich Series (Upper?)	Mt.Crosby, Queensland, Australia	Carnian
?Crosaphis virginiensis, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
SUBORDER BRACHYCERA/STEM GROUPS			
Gallia aelsatica Krzemiński, 2003	Grés-a-Voltzia	Vosges, France	Anisian
Prosechamyia trimedia, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian
Prosechamyia dimedia, n.sp.	Cow Branch Formation	Solite, Virginia, USA	Carnian-Norian

Fig. 1. Nick Fraser standing on an excavated section of the insect layer in the Cow Branch Formation from the Solite Quarry. The layer is a fine-grained black shale that dips northeast at 34°.

Dan River Jurassic-Triassic rift lake basin of the Eastern U.S. (LeTourneau and Olsen, 2003). Fossil insects from this deposit were first reported by Olsen et al. (1978), then by Fraser et al. (1996) based on abundant new material. Olsen's material is housed in the Peabody Museum of Natural History at Yale University, New Haven, CT (hereafter, "YPM"), and all other specimens are housed in the Virginia Museum of Natural History, Martinsville, VA (hereafter, "VMNH"). In the quarries there are outcrops of the upper part of the Carnian-aged (ca. 235–223 Ma) Cow Branch Formation (figs. 1, 2). This formation originated in one of a series of rift basin lakes created during the formation of Pangaea. Some of these ancient lakes reveal striking 21,000-year periods in sedimentation, caused by Van Houten cycles (Olsen, 1986; Witte et al., 1991). Van Houten cycles are cyclical changes in precipitation caused by Milankovitch-type orbitally driven changes in solar insolation (Olsen, 1986), whose periodicitiy is affected by the 21,000-year cycles in the precession of the equinoxes. Over 30 Van Houten cycles are preserved in the two main Solite quarries, and one cycle has proven to be particularly fossiliferous, including many insects (fig. 2).

The richest strata in the Solite quarries contain insects and the best-preserved plants and vertebrates, which also have the least bioturbation and the finest microlamination. Beard et al. (submitted) suggest the insect layer may reflect an environment in transition from ephemeral lake or bacterially matted lake margin to standing water marked by periodic carbonate precipitation. High CO_2 in the lake sediment may have rendered it toxic to scavengers and other benthic organisms, either directly or by promoting the growth of toxic algae. A modern analog may be the saline, alkaline dolomite lakes of South Australia. Insects are found in very fine-grained, black shales, preserved entirely as two-dimensional, silvery films composed of aluminosilicates with essentially no relief. Preservation of the insects is of microscopic scale, including microtrichia about 1 μm in thickness. The insects are preserved with a significant diversity of vascular land plants, including ferns, ginkgophytes, cycads, and abundant conifers and Bennettitales, which appear to be close relatives of conifers (Fraser et al., 1996; Axsmith et al., 1997). Insect diversity includes at least 11 orders of pterygote insects: Blattodea, Coleoptera, Diptera, Mecopterida, Odonata, Orthoptera, Plecoptera, Sternorrhyncha, Auchenorrhyncha, Heteroptera, and Thysanoptera, comprising perhaps 50 species known thus far (Fraser and Grimaldi, 1999, 2003). The Cow Branch Formation is the only significant deposit of Triassic insects from North America, and contains taxa that are among the oldest known records of Thysanoptera (Grimaldi et al., 2004), and certain families in several orders (e.g., Belostomatidae [Heteroptera], Staphylinidae [Coleoptera]).

The suggestion that the Cow Branch Formation "may be younger than judged from paleobotanical data" (Shcherbakov et al., 1995: 78) has little foundation, since the stratigraphy of the formation is well documented and correlated with other Late Triassic and Early Jurassic deposits of the
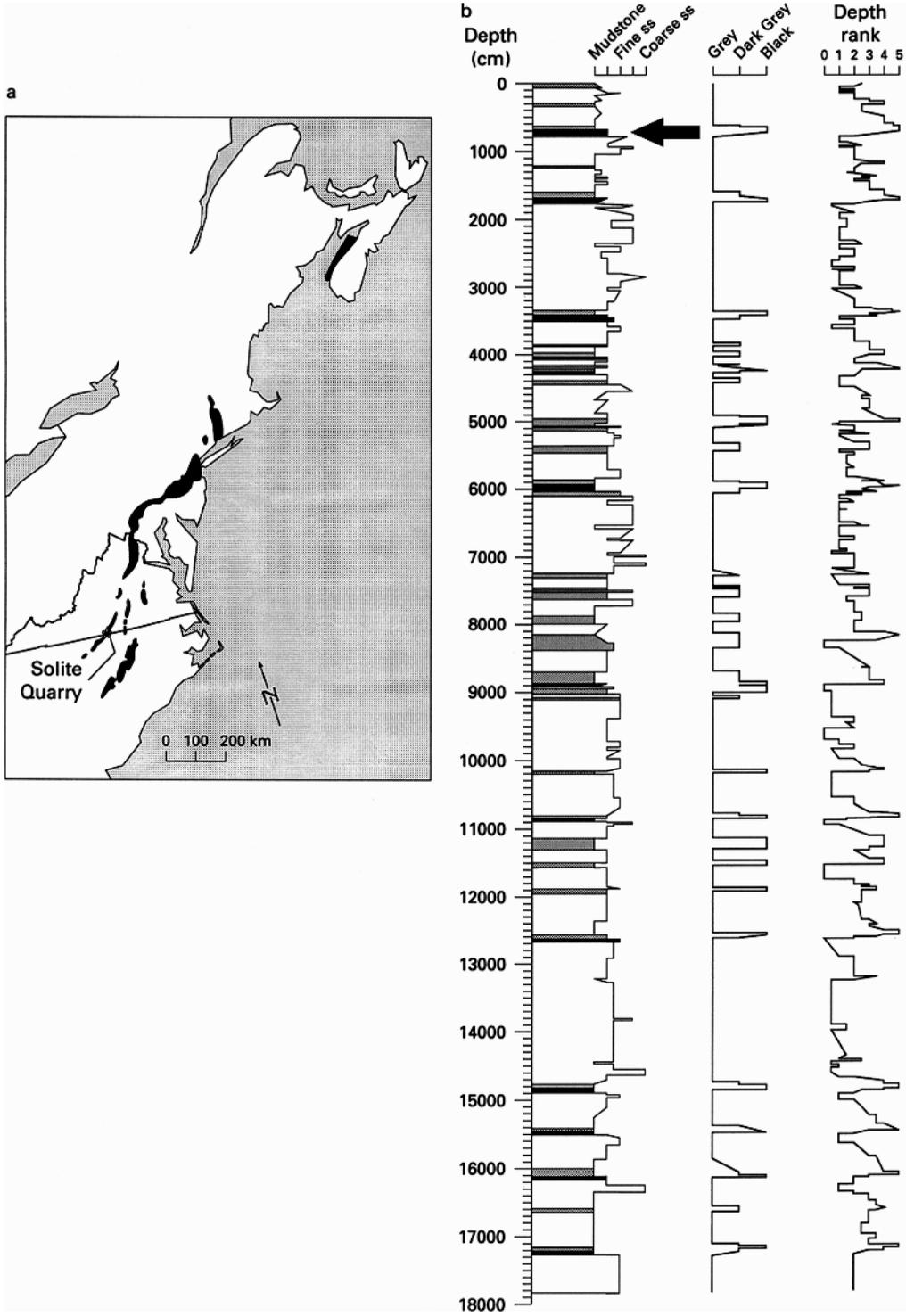
Fig. 2. Map and stratigraphy of the Triassic-Jurassic Newark Basin deposits. **a.** Map showing location of deposits, and of the Solite quarries. **b.** Stratigraphic sequence, with an arrow indicating the insect layer.

eastern North American rift valleys and with the Chinle Formation of the southwestern U.S., including the use of paleomagnetic dating (Olsen et al., 1978; Kent et al., 1995). The vertebrates in the assemblage also correlate with Carnian-aged vertebrates (Lucas and Huber, 2003), including the abundant amphibious protosaurian reptile *Tanytrachelos*. The age of the formation is Late Carnian, about 220 Ma.

MATERIALS AND METHODS

Perhaps the most significant feature of the Virginia Triassic deposits is their preservation. Where most other Triassic flies are known only as isolated and dissociated wings, the Virginia Triassic flies are mostly completely articulated. Having features of the legs (e.g., size of coxae, presence and size of tibial spurs) and head (e.g., structure of antennae) greatly improves phylogenetic inference. Proper study of the insects from the Solite quarries, however, requires wetting of the rock surface to improve contrast and an intense but diffuse light source. Specimens were wet with an evaporative solvent, generally 70% ethanol, then carefully blotted dry after study using a soft tissue. A fiberoptic ring light is absolutely necessary to illuminate the dim silvery images; directional light from fiber optic light guides do not adequately reveal details. Photography was done by attaching a ring light to a 1000 W output fiberoptic flash unit (MicrOptics, Inc.: ML-1000), and photographing with an Infinity K-2 long distance microscope and a Nikon D-1 digital camera (see www.microptics-usa.com). Wetted specimens were illustrated using a drawing tube attached to a stereoscope using ring-light illumination; use of polarizing film also helps.

SYSTEMATICS

INFRAORDER TIPULOMORPHA

Known as crane flies, the infraorder includes about 15,000 species in four living families: Tipulidae, Limoniidae, Cylindrotomidae, and Trichoceridae (the latter is sometimes placed near Psychodidae based on larval morphology). The Triassic family Vladipteridae, which has the most generalized venation among Diptera, also belongs here. Larvae of tipulomorphs are aquatic, semiaquatic or terrestrial, but usually associated with moist habitats, often found in decomposing plant material.

FAMILY LIMONIIDAE RONDANI, 1856

This is one of the largest families of Diptera with more than 11,000 Recent and 300 fossil species described (Evenhuis, 1994). The majority of Mesozoic limoniids belong to the basal subfamily Architipulinae Handlirsch.

Architipula youngi Krzemiński, 1992
figures 3a, 8a

Architipula youngi Krzemiński, 1992: 43.

In addition to the description of Krzemiński (1992) a faint pterostigma is observed at the apex of R_1 and R_2. Krzemiński indicated holotype collection number as 1103, but actually the specimen is registered under number YPM 35968. Three other paratypes are very poorly preserved. Specimen YPM 30077 can be identified as Tipulomorpha incertae sedis; specimen YPM 35973 (indicated as # 100000) is not conspecific with *Architipula youngi* since the fork R_{2+3} and R_4 is shorter than it's stem; specimen YPM 35969 lacks wings and could belong to Culicomorpha or Bibionomorpha as well as Tipulomorpha.

Metarchilimonia Blagoderov and Grimaldi, new genus

DIAGNOSIS: Small tipuloids with relatively wide wings; Sc short, approximately ½ the wing length. R_2 meets R_1. R_4 forms a stalk with R_5, *r-m* connects M_{1+2} and R_5. Crossvein *m-cu* connected to the base of fork of M_{3+4}.

TYPE SPECIES: *Metarchilimonia krzeminskorum* n.gen., n.sp.

DISCUSSION: The new genus is close to *Archilimonia* Krzemiński and Krzemińska, 2003, by virtue of a short Sc, a similar system of vein forks, *m-cu* close to the base of the fork of M_{3+4}. *Mabelisia* Shcherbakov and *Gnomusca* Shcherbakov, both from the Madygen Formation in Kyrgyzstan, also have
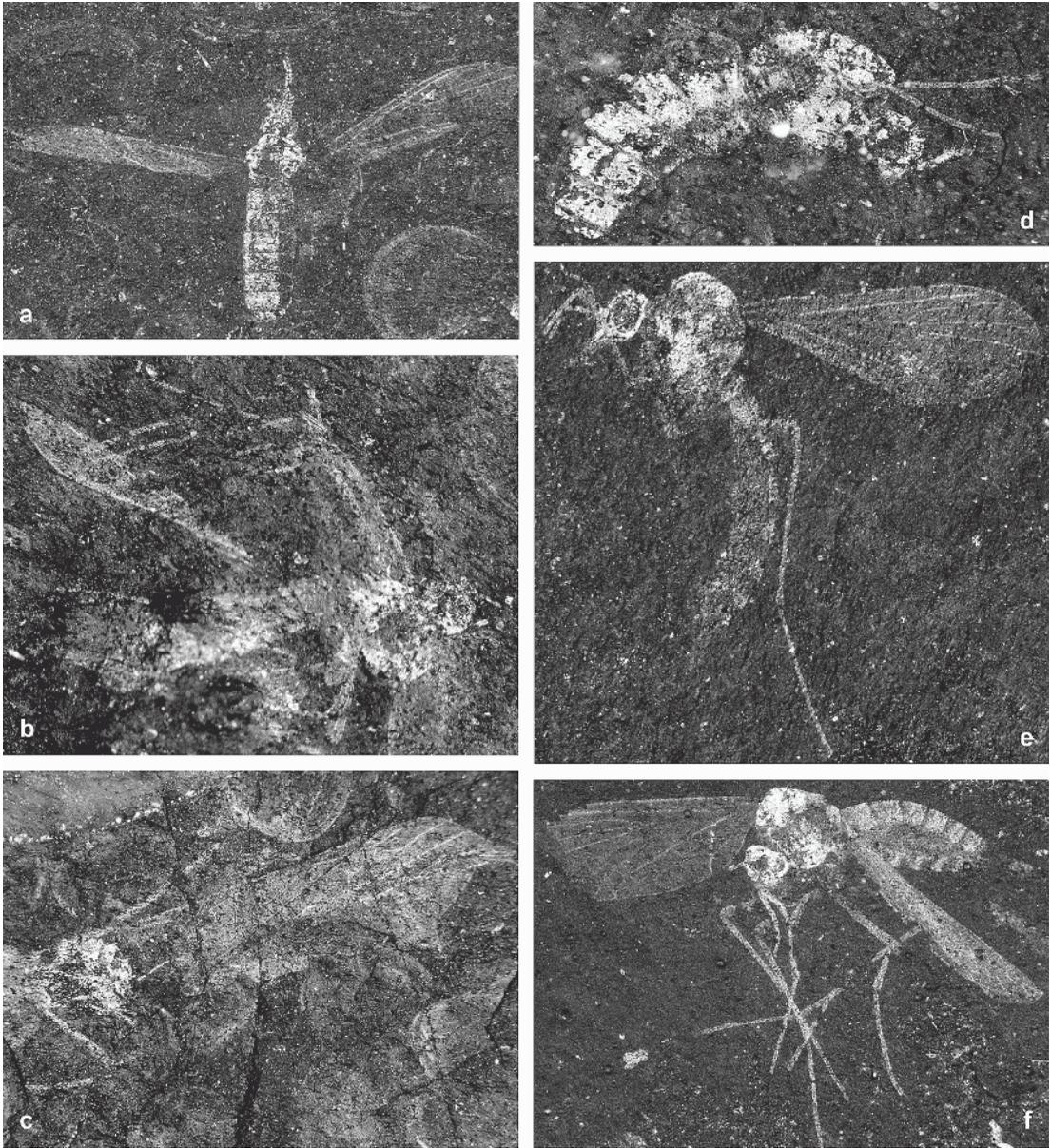
Fig. 3. Photomicrographs of tipulomorphan Diptera from the Late Triassic of the Cow Branch Formation, Solite Quarry. **a.** *Architipula youngi* Krzemiński, YPM 35986. **b.** Tipulomorpha indet., YPM 30077. **c.** Tipulomorpha indet., YPM 35973. **d.** Diptera indet., YPM 35969. **e.** *Metarchilimonia krzeminskorum* Blagoderov and Grimaldi, holotype VMNH 732. **f.** *Metarchilimonia krzeminskorum* Blagoderov and Grimaldi, paratype VMNH 3671. For size scales see fig. 8.

vein Sc rather short and have a similar structure of RS (at least in *G. renixa*), but they are significantly different in many other aspects of venation. *Metarchilimonia* differs from *Architipula youngi* Krzemiński, also from the Solite quarries, by the former having a wider wing, more proximal position of R_2, more distal position of *r-m* with respect to discal cell and the forking pattern of the radial veins.

ETYMOLOGY: From the Greek word με τ, meaning "after" or "next to", and *Archilimonia*. The name is feminine.

Metarchilimonia krzeminskorum
Blagoderov and Grimaldi, new species
figures 3e, f, 8c, d

DIAGNOSIS: Sc_2 preapical, discal cell shorter than fork of M_{1+2}.

DESCRIPTION: Female. Measurements: body length 4.7 mm, wing length 3.2 mm. Head round, antennae with 14 flagellomeres, gradually tapered in width toward apex. Scape short, smaller than basal flagellomere. Mouthparts forming rostrum, approximately $1.3\times$ greatest length of eye; palpi short (segmentation not preserved). Scutum arched. Wing moderately wide, width $0.39\times$ the length. Sc short, $0.53\times$ the wing length, ends slightly proximal to level of base of R_{2+3} stem. Sc_2 present, preapical. Base of stem of RS at $0.37\times$ the wing length. Five branches of RS, four reaching wing margin. R_2 meeting R_1 near wing margin. Stem of R_{2+3} parallel to R_1, slightly bent at base. R_{4+5} very short, $0.5\times$ the length of section of R_5 anterior to *r-m*. Base of R_5 transverse. Length of R_5 nearly $2\times$ longer than stem of RS. Basal fork of M at level of Sc apex. M_3 connected to M_{1+2} near the middle of stem of latter. Anterior margin of discal cell $1.3\times$ longer than stem of M_{1+2} and $0.8\times$ the length of M_1. Posterior margin of discal cell $0.7\times$ length of M_4. M_4 $1.6\times$ longer than stem of M_{3+4}. Crossvein *m-cu* in line with base of M_{3+4} fork. CuP and A veins not observed. Tibial spurs absent, legs with short setae. Oviscape as long as tergite 10, sclerotized, tarered at apex; cerci and valves not apparent.

MATERIAL: Holotype VMNH 732, sex unknown; paratype VMNH 3671, ♀.

ETYMOLOGY: The specific epithet is a patronym honoring Drs. Wiesław Krzemiński and Ewa Krzemińska, for their significant contributions to the study of early Diptera.

Metarchilimonia solita
Blagoderov and Grimaldi, new species
figures 4a, 8b

DIAGNOSIS: Differs from *M. krzeminskorum* by being nearly half the size, and by

various venation features: stem of M_{1+2} longer than the fork of M_{1+2} (vs. longer fork); apical Sc_2; discal cell longer.

DESCRIPTION: Measurements: body length 2.3–2.5 mm (holotype, 2.5), wing length 2–2.2 mm (holotype, 2.2). Head round, rostrum not observed. Antenna moniliform, 14-segmented, flagellomeres very slightly tapered toward apex, each with single apical seta. Only basal 8 flagellomeres well preserved. Legs densely setose, without tibial spurs. Sc short, $0.46\times$ the wing length. Sc_2 apical, its length about equal to short, distal segment of Sc_1. Base of R_5 oblique. Anterior margin of discal cell $1.2\times$ longer than stem of M_{1+2} fork and $1.2\times$ longer than M_1. Posterior margin of discal cell $1.2\times$ longer than M_4.

MATERIAL: Holotype VMNH 3013.

ETYMOLOGY: The specific epithet is for the Solite Corporation, which has quarried the locality.

INFRAORDER PSYCHODOMORPHA

This infraorder includes the living families Tanyderidae and Psychodidae, and sometimes Ptychopteridae, the Blephariceromorpha, and Scatopsoidea. The first two families are known from the Early Jurassic (Ansorge, 1994). Psychodidae are widely distributed and their larvae breed in wet to foul substrates. Phlebotominae feed on vertebrate blood and insect hemolymph. In the widest sense this infraorder may include the following extinct taxa: Hennigmatidae, Tillyardipteridae, Rhaetaniidae, and Eoptychopteridae.

FAMILY PSYCHODIDAE NEWMAN, 1834, OR NEAR

Triassopsychoda Blagoderov and Grimaldi, new genus

DIAGNOSIS: Wing drop-shaped, with highly reduced anal lobe; veins with long setae. Vein Sc meets C, ends slightly distad of basalmost fork of R. Vein R with four branches, M with three branches, *m-m* absent; bases of R_{4+5}, R_5, *r-m* in apical half of wing; base of M faint.

TYPE SPECIES: *Triassopsychoda olseni* n.sp.

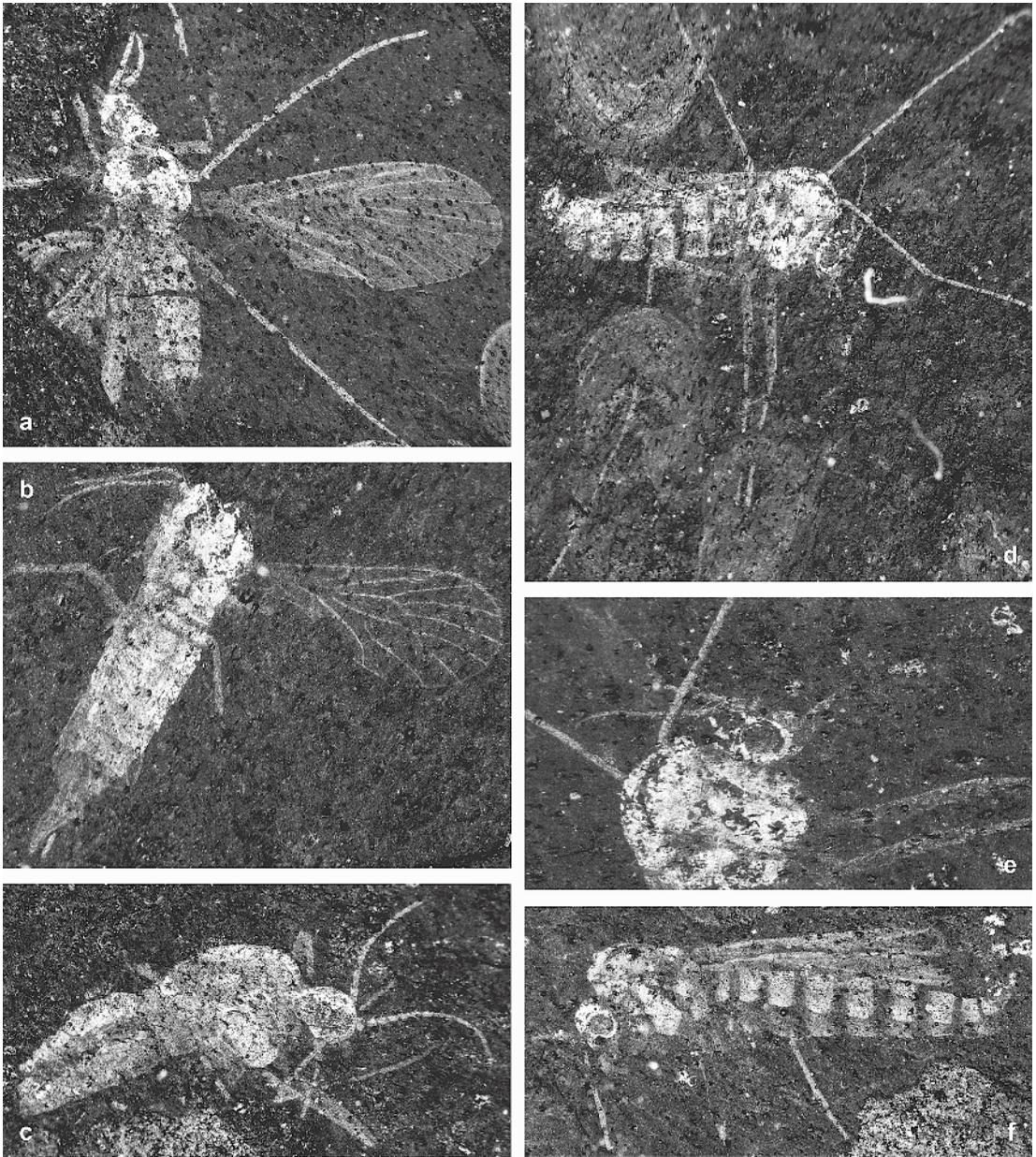ETYMOLOGY: The genus name is from the Triassic; the name is feminine.

Fig. 4. Photomicrographs of tipulomorphan (a), psychodomorphan (b), and culicomorphan (c–f) Diptera from the Cow Branch Formation. **a.** *Metarchilimonia solita* Blagoderov and Grimaldi, holotype VMNH 3013. **b.** *Triassopsychoda olseni* Blagoderov and Grimaldi, holotype VMNH 733. **c.** Culicomorpha indet., VMNH 808. **d.** Culicomorpha indet., VMNH 951. **e.** Culicomorpha indet., VMNH 951, detail of head, showing proboscis. **f.** Culicomorpha indet., VMNH 932. For size scales see fig. 9.

Triassopsychoda olseni
Blagoderov and Grimaldi, new species
figures 4b, 9a

DIAGNOSIS: As for genus.

DESCRIPTION: Female. Measurements: body length = 2.1 mm, wing length = 1.4 mm. Head round, eyes reniform, with large facets. Length of mouthparts, including palps, approximately ¼ height of head. Antennae with 14 flagellomeres, each with whorl of long setae; length of each flagellomere approximately $2\times$ its width. Apex of wing broadly rounded, anal lobe absent, wing base petiolate. Wing veins with long setae including C. Costal cell very wide; Sc meets C, its length approximately $0.4\times$ the wing length. Base of RS stem at $0.35\times$ wing length, base of R_{3+4+5} fork at $0.53\times$ the wing length, so radial-medial cell is long and wide. R_2 lost, base of R_{4+5} fork distal to base of R_3. Lengths of stem of R_{4+5} fork, basal section of R_5, *r-m*, and stem of M_{1+2} fork are subequal. Base of M_{3+4} is at $0.47\times$ the wing length. Veins M_3 and *im* absent; discal cell open and very wide. Nine segments of abdomen apparent, subequal in length. Cerci/oviscapt long, narrow, triangular, length equal that of segments 8 and 9 combined.

MATERIAL: Holotype VMNH 733.

ETYMOLOGY: The species epithet is in honour of Dr. Paul Olsen of Lamont-Doherty Earth Observatory, who has done the original work on the Solite quarry fossils, and who has brought tremendous insight to the Mesozoic rift basins of eastern North America.

DISCUSSION: Despite the reduced venation (absence of R_2, M_3, base of M) this fly possesses some very plesiomorphic features: the distal positions of the base of RS, and radial and medial forks, and crossveins *r-m* and *m-cu*, and a very wide discal cell. The structure of the radial veins of the new genus resembles the living genus *Horaiella* Tonnoir from India and especially *Eatonisca* Meunier from Baltic amber (both Psychodidae), but differs from those genera by the distal position of the radial and medial forks and the absence of M_3. It differs from the Early Jurassic genera *Tanypsycha* Ansorge, *Liassopsychodina* Ansorge, and *Libanophlebotomus* Azar et al.,

1999, by the absence of veins R_2 and M_3, from the latter genus also by having Sc merging with C instead of R_1.

The position of *Triassopsychoda* is uncertain. The reniform eye shape, setal whorls on the flagellomeres, long cerci/oviscapt, broad wing with narrow stem, reduced anal lobe, and setose wing veins are, in combination, diagnostic of Psychodidae. The striking feature of *Triassopsychoda*, distinguishing it from other Psychodidae is a complete loss of vein M_3 while preserving crossvein *tb* (the basalmost section of M_4,). Many authors, following McAlpine (1981) interpret the posterior longitudinal vein in the hind medial fork as CuA_1 (Azar et al., 1999; Duckhouse, 2000). As we discuss below (see Phylogeny), CuA in Diptera is always a nonbranched convex vein. In Psychodidae, however, vein relief is unapparent, veins tend to be equally sclerotized and the membrane weakly corrugated; longitudinal veins are long and parallel; and crossveins and fork bases are shifted proximad. *Triassopsychoda*, conversely, has CuA long and thick, just like in other Diptera, and the base of M_4 is at the middle of the wing. Another objection against including *Triassopsychoda* in Psychodidae is the structure of vein C, which is evanescent slightly apical to the apex of R_5 (vs. circumambient in Psychodidae, although this state may be plesiomorphic because some Tipulomorpha share it). Thus, despite the highly reduced venation, *Triassopsychoda* possesses several plesiomorphies not found in living Psychodidae.

INFRAORDER CULICOMORPHA

Culicomorpha include more than 12,000 Recent species in eight families: Ceratopogonidae, Chaoboridae, Chironomidae, Corethrellidae, Culicidae, Dixidae, Simuliidae, and Thaumaleidae. The Culicidae, Corethrellidae, Simuliidae and basal Ceratopogonidae are essentially hematophagous. Larvae of almost all culicomorphs are aquatic or live in moist habitats. About 300 fossil species are described, about 60% of which are Ceratopogonidae. The earliest known fossil of the infraorder is *Aenne* from the uppermost Triassic of England, which has been assigned

to the Chironomidae (Krzemiński and Jarzembowski, 1999).

Culicomorpha *indet.*
figures 4c–f, 5a, b, 9b, c

Several specimens from the Solite quarries have their venation obscured, so they can not be described and named formally. Some of these specimens, however, are otherwise exquisitely preserved, retaining some distinctive features that allow placing them within the infraorder Culicomorpha. Despite differences in sizes and leg lengths, specimens VMNH 808, 873, 932, 951, 2956, and 3056 possess: (1) slender moniliform antennae with long setae on each flagellomere; (2) a round antennal pedicel that is larger than the scape; (3) round (vs. reniform or emarginate) eyes with large facets; (4) a broad katepisternum that is rounded ventrally; (5) a short, arched mesonotum that nearly overhangs the pronotum; (6) small, unprotruding scutellum; (7) wide insertion of the abdomen; and (8) male genitalia curved dorsally. Features 2, 5, and 8 are particularly distinctive to Culicomorpha, but venation is needed to confirm this. Most significantly, VMNH 951 bears a long, slender proboscis that is nearly twice as long as the head height (figs. 4d, e; 9b, c).

Body and leg proportions of VMNH 951 are very similar to that of other culicomorphans (VMNH 808, 873, 932, 2956, 3056), but it is doubtful that the specimens are conspecific, since there are no known instances in any living species of Diptera where a proboscis is so dramatically dimorphic. In various Recent species of biting midges the styletlike mandibles of females are well developed and used to puncture the skin of their host in order to feed on blood; males feed on nectar and have vestigial mandibles, but the proboscis size barely differs with that of females. Since angiosperms did not appear until nearly 100 Ma later, it is possible that the proboscis was used to probe Bennettitalean or Gnetalean reproductive structures, and bennettitaleans occurred in the Triassic of Virginia. Recent Gnetales produce pollination droplets, on which insects feed, but these are external, making a long proboscis unnecessary. VMNH 951 is the earliest fossil evidence

of a structure in Diptera specialized for blood feeding, in a group in which the ground-plan adult diet is hematophagy (Grimaldi and Engel, 2005; Lukashevich and Mostovski, 2003). If this is the case, VMNH 951 is the earliest known blood-feeding insect. It is not until the Jurassic that definitive insect ectoparasites appeared, and not until the Cretaceous that definitive hematophagous insect groups appeared (Grimaldi and Engel, 2005).

INFRAORDER BIBIONOMORPHA

The composition of the infraorder is in flux, partly because it is paraphyletic with respect to the higher flies, the Brachycera. It includes diverse Mesozoic taxa, such as Eliidae and various families of sciaroids, in addition to the families discussed below. The infraorder also includes very diverse Recent families, such as Mycetophilidae and Cecidomyiidae, totaling 8,000 species in some 25 families. In contrast to the other major infraorders of nematocerous flies, larvae of Bibionomorpha and those of their stem group (the Brachycera) are almost exclusively terrestrial, being saprophagous, fungivorous, phytophagous, and sometimes predatory.

FAMILY PROCRAMPTONOMYIIDAE KOVALEV, 1985

A small family of basal bibionomorphs known from Late Triassic to Early Cretaceous of North America, Australia, Asia, and Europe. Kovalev (in Kalugina and Kovalev, 1995) referred the family to Anisopodoidea based on the presence of a discal cell. However, a more accurate placement would be at the base of all Bibionomorpha s.l. (Shcherbakov et al., 1995).

Genus *Yalea* Krzemiński, 2004

Yala Krzemiński, 1992: 44. Type species: *Yala argentata* Krzemiński, 1992, monotypic, by original designation (preoccupied by *Yala* Chu, 1979 [Geometridae]).
Yalea Krzemiński, 2004: 229. Replacement name.

DIAGNOSIS: R_4 base proximal to *r-m*, section of M_2 proximal to *m-m* and section of M_3 proximal to *m-m* are nearly equal, with length 0.3–0.5$\times$ that of discal cell.
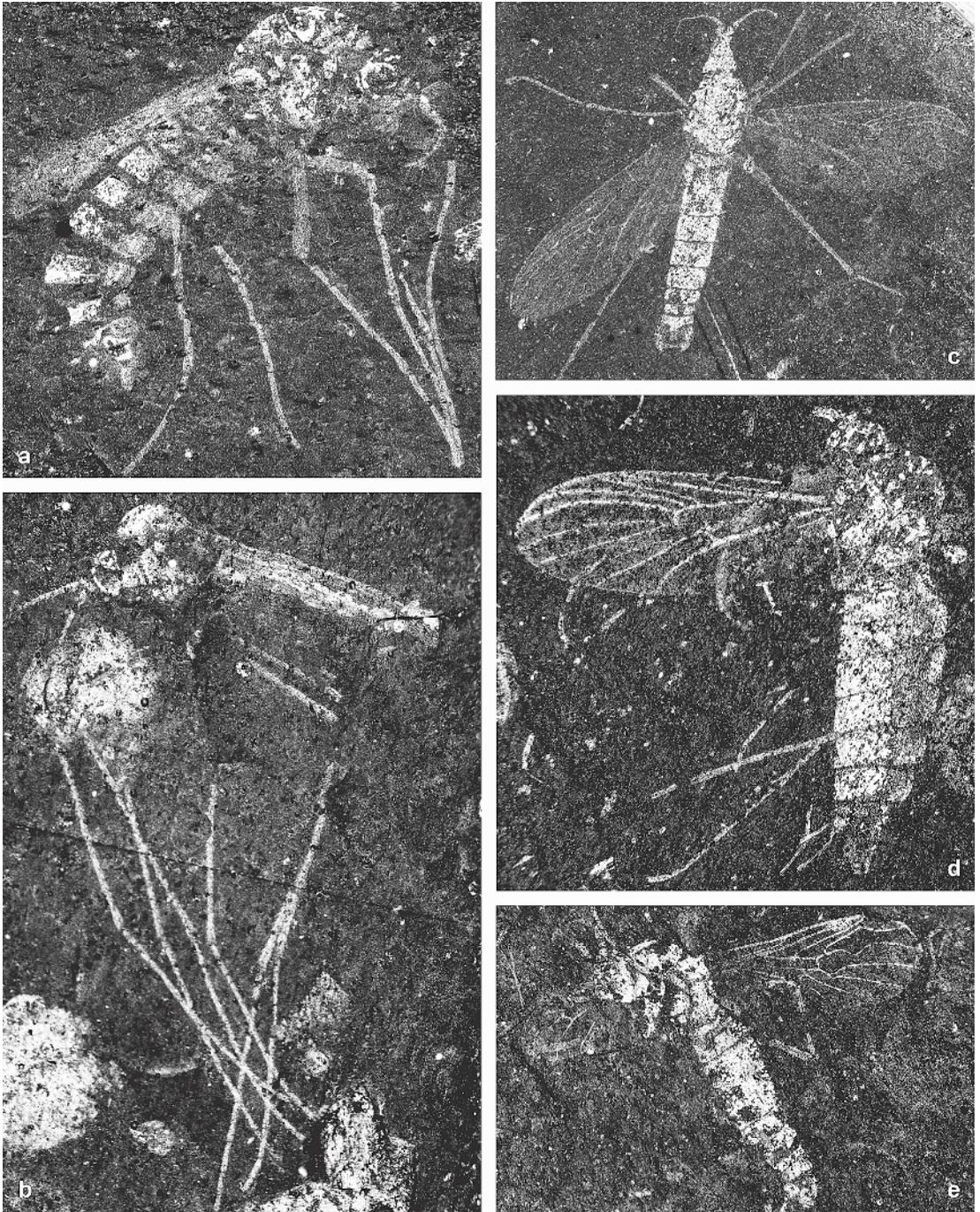
Fig. 5. Photomicrographs of culicomorphan (a, b) and bibionomorphan (c–e) Diptera from the Cow Branch Formation. **a.** Culicomorpha indet., VMNH 2956. **b.** Culicomorpha indet., VMNH 3056. **c.** *Yalea argentata* (Krzemiński). **d.** *Yalea rectimedia* Blagoderov and Grimaldi, VMNH 1041. **e.** *Veriplecia rugosa* Blagoderov and Grimaldi, YPM 35989. For size scales see fig. 10.

INCLUDED SPECIES: *Yalea argentata* (Krzemiński) (figs. 5c, 10b) and *Y. rectimedia* Blagoderov and Grimaldi, new species.

Yalea rectimedia Blagoderov and Grimaldi, new species
figures 5d, 10a

DIAGNOSIS: Nearly $0.7\times$ smaller than *Yalea argentata*. Sc shorter, ends at the level of R_{2+3} base (vs. slightly distad). M_3 and M_4 parallel (vs. slightly divergent and curved). R_{2+3} $2\times$ the length of stem of RS (vs. $1.5\times$ the length). Length of M_{1+2} stem equal to section of M_2 proximal to *m-m* (vs. $1.5\times$ the length).

DESCRIPTION: Female. Measurements: body = 3.8 mm, wing = 2.2 mm. Scape and pedicel wider than flagellum, hemispheric; flagellomeres cylindrical, with lengths about equal to widths. Sc ends at C at level of base of R_{2+3}. R_1 almost straight, R_{2+3} sigmoid, curved anteriorly at apex. R_4 and R_5 curved posteriorly. R_{2+3} $2\times$ the length of the basal section of RS. Length of basal section of RS $2.5\times$ that of section of RS between bases of R_{2+3} and *r-m*. M stem weak. Section of M_{1+2} stem proximal to *r-m* $2.3\times$ the length of stem section distal to *r-m*; length of M_1 and M_2 fork $3.5\times$ that of M_{1+2} stem. Apex of CuA distal to level of *r-m* crossvein. Cerci apparently one-segmented.

MATERIAL: Holotype VMNH 1041.

ETYMOLOGY: The species epithet is from the Latin *rectus*, meaning "straight", in reference to details of wing venation.

Genus *Alinka* Krzemiński, 1992

Alinka Krzemiński, 1992: 46. Type species: *Alinka cara* Krzemiński, 1992, monotypic, by original designation.

Krzemiński (1992: fig. 16) described *Alinka cara* as the earliest representative of Brachycera known at the time. This opinion was later critiqued by Shcherbakov et al. (1995), Grimaldi and Cumming (1999), and others. Our re-examination of the holotype (YPM 16826 [not 100 000 as originally cited]) supports the placement of *Alinka* in the family Procramptonomyiidae. Eleven flagellomeres are preserved in the antenna, although the actual number could be greater because the apical flagellomere is incomplete and without the apical tuft of setulae originally reported (Krzemiński, 1992: fig. 6a). The only synapomorphy of *Alinka* with Brachycera was a short R_4, but this character state appears several times in Diptera, such as in Paraxymyiidae, Eoditomyiidae, and Protorhyphidae (see below). The paratype of *A. cara* is too poorly preserved to be identified as a conspecific with certainty.

SUPERFAMILY SCIAROIDEA BILLBERG, 1820
FAMILY PARAXYMYIIDAE ROHDENDORF, 1946

This family includes basal sciaroids ("fungus gnats") with three branches of RS and a distinct, though sometimes faint base of M. We are including in this family the Eomycetophilidae Ansorge, 1996, which is apomorphic in having R_4 very short, apical, and transverse. We consider this family to be a subfamily of Paraxymyiidae. Four genera of Paraxymyiidae are known from the Late Triassic to the Early Cretaceous: *Paraxymyia* Rohdendorf, 1946; *Veriplecia* Blagoderov, 1999; *Eomycetophila* Kovalev, 1990; and *Complecia* Blagoderov, 1999.

Genus *Veriplecia* Blagoderov, 1999

Veriplecia Blagoderov, 1999: 12. Type species: *V. clara* Blagoderov, 1999, monotypic.

Veriplecia rugosa Blagoderov and Grimaldi, new species
figures 5e, 10d

DIAGNOSIS: Differs from *Veriplecia clara* from the Late Triassic of Australia by the more basal position of the base of R_{2+3}, which is slightly basal to the level of crossvein *tb* (basal section of M_{3+4} stem proximal to crossvein *m-cu*).

DESCRIPTION: Male. Measurements: body = 3.1 mm, wing = 2.2 mm. Head round, eyes large, genae setulose. Antennae moniliform, with scape slightly larger than individual flagellomeres. Scutum with fine setulae; no large, bristlelike setae. Costa setulose. Sc short, $0.41\times$ the length of wing, ends at C slightly proximal to level of base of R_{2+3}. Sc_2 not apparent or absent. Ratios of length of stem of RS: stem of R_{4+5}: R_5 are 1:1:3.

Crossvein r-m located between bases of R_{2+3} and R_4; length of section of RS between r-m and base of R_4 is $0.5\times$ the length of section between bases of R_{2+3} and r-m. Distinct pterostigma at apex of R_1. Ratios of lengths of M stem, and sections of M_{1+2} proximal and distal of r-m when straightened out are 5:1:1. Basal stem of M evanescent toward wing base. Length of M_1 and M_2 fork $5.7\times$ the length of stem of M_{1+2} distal to r-m. Length of M_{1+2} stem proximal to r-m is $2.6\times$ the tb length. Crossvein m-cu is $1.7\times$ the length of tb. CuA very slightly curved back. 10 visible segments of abdomen; segment 3 largest, 8 smallest, 10 apparently large, covering ventrally situated genitalia. Abdomen and genitalia setose. Pair of short, protruding appendages present (probably gonostyli).

MATERIAL: Holotype YPM 35989.

ETYMOLOGY: The specific epithet is from the Latin *rugosus*, meaning ''wrinkled'', in reference to the deformed wing of the unique specimen.

Virginiptera Blagoderov and Grimaldi, new genus

DIAGNOSIS: Costa ends slightly beyond tip of R_5. Sc ends at C distal to the base of RS and at the level of base of fork R_{2+3}–R_{4+5}. R and CuA considerably thicker than M. Base of R_{2+3} proximal to crossvein r-m. R_4 very short, $0.5\times$ the length of RS. Stem of M weak, incomplete. Crossvein tb very short. CuA evenly curved. Tibial spurs (1:1:2) present, length ca. $1.3\times$ width of tibia. Female cerci 2-segmented. Male genitalia held ventrally.

The new genus is close to *Complecia clara* Blagoderov, 1999, from the Late Triassic of Australia, which differs from the new genus in having Sc shorter and ending free, base of R_{2+3} very close to the base of r-m, and a more regular spacing of veins in the radial sector (ratios of the distances along C between tips of R_1, R_{2+3}, and R_5 are 1.3:1.1:1.0) and in the medial sector (ratios of the distances along wing margin between apices of R_5, M_1, M_2, M_{3+4}, and CuA are 1:1.3:1.6:1.9).

TYPE SPECIES: *Virginiptera certa*, new species.

ETYMOLOGY: The genus name derives from Virginia, the U.S. state of origin of the fossil. The genus name is feminine.

COMMENTS: The new genus has a venation similar to that of Paraxymyiidae (Eomycetophilinae) and Eoditomyiidae: three branches in RS, with R_4 extremely short, the base of R_{2+3} proximal to r-m, three branches of M, and the discal cell reduced. *Virginiptera* differs from *Eoditomyia* Ansorge (Early Jurassic, Germany) by having a complete Sc, and in *Eoditomyia* crossveins r-m, tb and m-cu are nearly in line, and the base of M is completely reduced. It differs from *Crosaphis* (Anisopodoidea) by the presence of a short R_4 vein.

The new genus is closely related to or within Sciaroidea based on the following features:

- Length of coxae approximately equal to thoracic height. Anisopodoidea in general have much shorter coxae (length ca. $0.3\times$ the depth of thorax) than in Sciaroidea, the latter of which have a coxal length that may even exceed the thoracic height.
- Tibial spurs as long as the tibial diameter, and protruding at approximately $45°$. Sciaroidea have short to extremely long tibial spurs, but the position is always protruding away from the tibia. In contrast, Anisopodoidea (including fossil Anisopodidae and Protorhyphidae) have short tibial spurs in line with the tibia.
- CuA is evenly curved. In most Anisopodoidea the section of CuA distal to m-cu is apomorphically straight or sinuous.
- Abdominal tergite I lacks laterodorsal tubercles or protrusions. Sciaroidea never possess these structures.
- Anepisternum is bare. In those fossil Sciariodea for which preservation allows observation, as well as in many basal Recent sciaroids, the pleural sclerites are bare. Anisopodoidea very often have the setose pleural sclerites.
- Segment 8 is short in females. Size of the eighth segment varies in Sciaroidea and Anisopodoidea, but it is generally reduced in the former and well developed in the latter group.
- Tibiae with rows of thick dorsal setae. Anisopodoidea usually lack thick setae on the tibiae.
- MA or arculus not seen at the wing base. Anisopodoidea have a strong veinlike arculus; in Sciaroidea MA is usually

represented only by a kink in the wing membrane at the base of R.

Virginiptera certa Blagoderov and Grimaldi, new species
figures 6b, 11c

DIAGNOSIS: Sc ends at C, very slightly proximal to base of R_{2+3} and distal to crossvein tb. Crossvein r-m as long as section of RS between bases of R_{2+3} and r-m. Stem of M slightly kinked at r-m and tb. Length of section of M_{1+2} proximal to r-m 1.6× that of r-m. Section of M_{1+2} stem distal to r-m with length 1.8× that of r-m.

DESCRIPTION: Measurements: body length = 2.8–3.1 mm (holotype 3.1 mm), wing length = 1.9–2 mm (holotype 1.9 mm), antennal length = 0.6 mm. Antennae short, approximately 0.7× thorax length; flagellum 14-segmented (13-segmented in VMNH 2998); flagellomeres cylindrical, length of each ca. 0.5× the width. Scutum with short irregular setulae, no bristlelike setae, several longer setae caudally. Scutellum small, not protruding. Katepisternum wider than deep. Abdomen setulose, attachment slightly narrowed; widest at segments 3–4. Length of segment 8 0.5× that of segment 7. Cerci 2-segmented. **Wing:** Costa ends slightly beyond tip of R_5, ½ the length between tips of R_5 and M_1 on holotype's left wing. Sc ends at C, slightly proximal to base of R_{2+3} and distal to crossvein tb. Sc length 0.4× the wing length. R and CuA veins distinctly thicker and more sclerotized than medial veins. R_1 length 0.67× the wing length. R_{2+3} nearly parallel to R_1, both veins very slightly curved toward anterior margin of wing. R_4 very short, straight, 0.5× the length of R_5. Ratios of distances between tips of R_1, R_{2+3}, and R_5 on C are 2:2.5:1. R_{4+5} stem straight basally, in apical quarter curved slightly backward, ending at wing tip. Crossvein r-m as long as section of RS between bases of R_{2+3} and r-m. Stem of M slightly kinked at r-m and tb; M_{1+2} stem proximal to r-m is very weak. Section of M_{1+2} stem distal of r-m 1.8× that of section proximal to r-m. Length of section of M_{1+2} proximal to r-m 1.6× that of r-m. Length of M_1–M_2 fork 4.2× the length of section of M_{1+2} distal to r-m. Ratios of distances at wing margin between apices of R_5, M_1, M_2, M_{3+4},

and CuA are 1:1.5:2.5:2.5. Crossvein tb very short, but distinct. CuA evenly curved. Legs setulose, hind tibiae with distinct row of dorsal setae. Tibial spurs 1.5× the tibial diameter, protruding 45° from axis of tibia.

MATERIAL: Holotype VMNH 731, ♀; paratype VMNH 2998, ♂.

ETYMOLOGY: The species epithet is from the Latin *certus*, meaning "certain".

Virginiptera similis Blagoderov and Grimaldi, new species
figures 6d, 11b

DIAGNOSIS: Size slightly less than half that of *V. certa*. Sc ends at C, at the level of crossvein tb and significantly proximal to level of r-m. Crossvein r-m 2× longer than section of RS between bases of R_{2+3} and r-m. Length of section of M_{1+2} proximal to r-m is 1.3× that of r-m. Length of section of M_{1+2} distal to r-m is 2× that of M_{1+2} section proximal to r-m.

DESCRIPTION: Measurements: body = 1.3 mm, wing = 1.3 mm, antenna = 0.7 mm. Flagellum 14-segmented, flagellomeres cylindrical. Scutum arched. Abdomen with male terminalia large and folded under apex of abdomen. **Wing:** Costa ends slightly beyond tip of R_5. Sc ends at C, at level of crossvein tb. Length of Sc 0.42× the wing length. Sc_2 preserved. Length of R_1 0.6× the wing length. R_{2+3} nearly straight, curved at apex toward anterior margin of wing. Ratios of distances between tips of R_1, R_{2+3}, and R_5 on C are 1.5:2.5:1. R_5 short, straight; R_4 slightly curved, 0.5× length of R_5. Crossvein r-m 2× longer than section of RS between bases of R_{2+3} and r-m. Stem of M nearly straight, base evanescent. Length of M_{1+2} section proximal to r-m 1.3× that of r-m. Length of section of M_{1+2} distal to r-m is 2× that of section of M_{1+2} proximal to r-m. Length of M_1 and M_2 fork is 4× the length of M_{1+2} section distal to r-m. Crossvein tb very short, but distinct. Ratios of distances between apices of R_5, M_1, M_2, M_{3+4}, and CuA at wing margin are 1:1.5:2:2. CuA evenly curved.

MATERIAL: Holotype VMNH 825, ♂; paratype VMNH 1042, ♂.

ETYMOLOGY: The species epithet is from Latin *similis*, meaning "similar to" or "resembling".
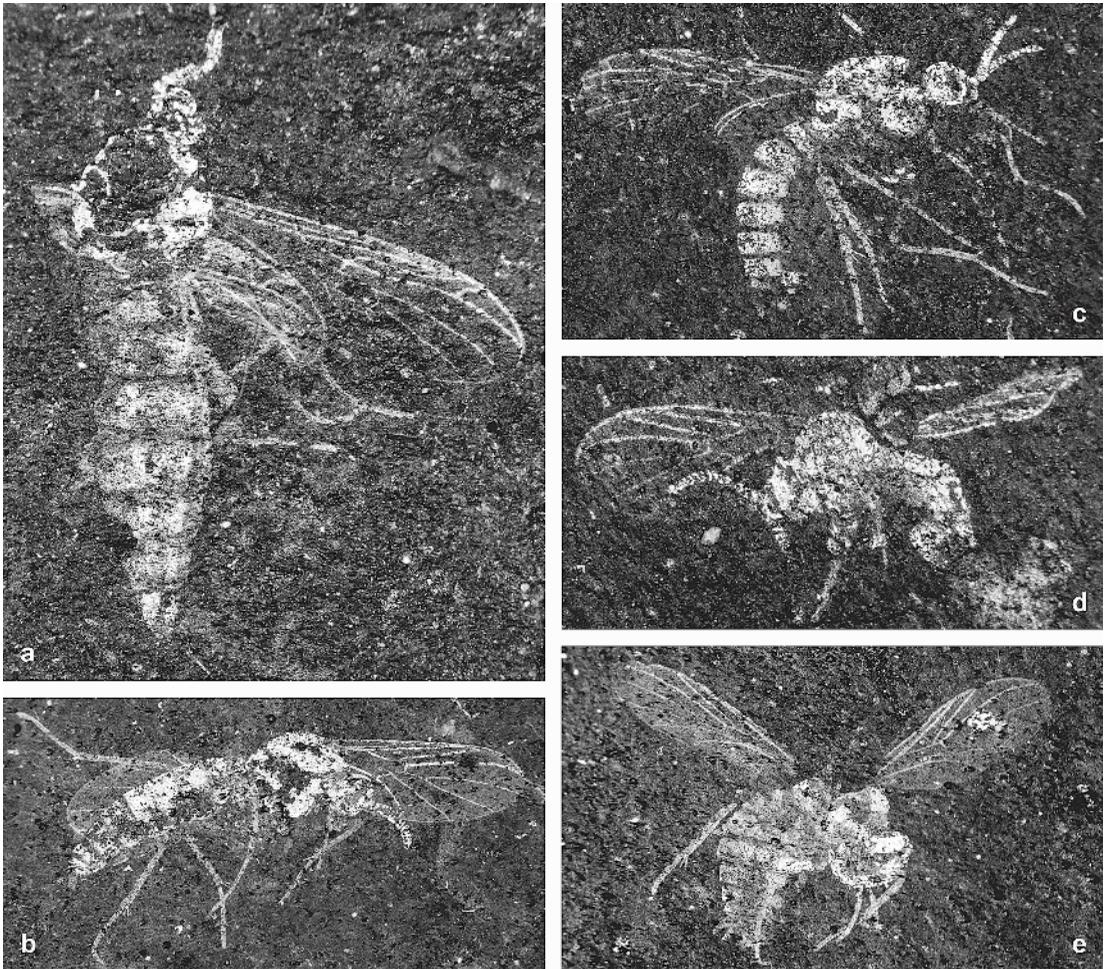
Fig. 6. Photomicrographs of bibionomorphan Diptera from the Cow Branch Formation. **a.** *Alinka cara* Krzemiński, YPM. **b.** *Virginiptera certa* Blagoderov and Grimaldi, holotype VMNH 731. **c.** *Virginiptera certa* Blagoderov and Grimaldi, paratype VMNH 2998. **d.** *Virginiptera similis* Blagoderov and Grimaldi, VMNH 825. **e.** *Virginiptera lativentra* Blagoderov and Grimaldi, holotype VMNH 2923. For size scales see fig. 11.

Virginiptera lativentra
Blagoderov and Grimaldi, new species
figures 6e; 11d

DIAGNOSIS: Sc very short, ends at C slightly proximal to base of *m-cu*. C ends well beyond tip of R_5, almost to tip of M_1. Crossvein *r-m* as long as section of RS between bases of R_{2+3} and *r-m*. Length of section of M_{1+2} proximal to *r-m* 1.4× that of *r-m*. Length of section of M_{1+2} distal to *r-m* 1.8× the length of section proximal to *r-m*; M_{3+4} connects directly to stem of M.

DESCRIPTION: Measurements: body = 2.2 mm, wing = 1.6 mm, antennae = 0.8 mm. Palpi 5-segmented, long, length nearly equal to length of head. Flagellum 14-segmented, flagellomeres cylindrical. Tibial spurs 1.5× the tibial diameter, hind tibia with a row of dorsal bristles, fore tibia with one apical spur, hind tibia with two, midtibial spurs obscured. Abdominal tergite 4 longest

and widest. Seventh segment short, $0.5\times$ the sixth; eighth segment very short, retracted. Ninth tergite with two triangular dorsal processes. **Wing:** Costa ends beyond tip of R_5 at 2/3 the length between tips of R_5 and M_1. Length of Sc $0.31\times$ the wing length. Sc ends at C proximal to *m-cu*. R_1 $0.54\times$ the wing length. R_1 and R_{2+3} nearly parallel, straight. Ratios of distances between tips of R_1, R_{2+3}, and R_5 along C are 1.2:1.6:1. R_{4+5} stem and R_{2+3} divergent for entire length. R_4 short, straight, $0.5\times$ length of R_5. Crossvein *r-m* as long as section of RS between bases of R_{2+3} and *r-m*. Stem of M weak, but can be traced nearly to base of wing. Length of section of M_{1+2} stem proximal to *r-m* $1.4\times$ that of *r-m*; section distal to *r-m* $3.4\times$ that of *r-m*. Fork of M_1 and M_2 $3.7\times$ longer than its stem. Crossvein *tb* absent, *m-cu* touches M stem. Ratios of distances between apices of R_5, M_1, M_2, M_{3+4}, and CuA at wing margin are 1:1.3:1.4:2.5. CuA evenly curved.

MATERIAL: Holotype VMNH 2923, VMNH 914, ♂ (part and counterpart).

ETYMOLOGY: The species epithet is from Latin *latus*, meaning "wide". and *venter*, meaning "abdomen".

SUPERFAMILY ANISOPODOIDEA KNAB, 1912

The superfamily includes about 200 species in three small families: Mesozoic Protorhyphidae, Jurassic-Recent Anisopodidae sensu lato, and Triassic Crosaphididae. It is often believed to be the living sister group to the Brachycera (Woodley, 1989; Oosterbroek and Courtney, 1996).

FAMILY PROTORHYPHIDAE HANDLIRSCH, 1906

Brachyrhyphus Blagoderov and Grimaldi, new genus

DIAGNOSIS: Sc $0.45\times$ the wing length, ends at C slightly beyond the level of the basal fork of M, level with base of R_{2+3}. R_{2+3} slightly converging with R_1; R_4 $0.25\times$ the length of stem of R_{4+5}, $0.28\times$ length of R_5, almost straight. M stem faint, crossvein *m-m* connects M_2 and M_3. CuA evenly curved posteriad. The new genus differs from all known Protorhyphidae by the very short vein R_4.

TYPE SPECIES: *Brachyrhyphus distortus* n.sp.

ETYMOLOGY: The genus name is from the Greek βραχς, meaning "short", and *Rhyphus* (a generic name in the family), in reference to the short R_4. The name is masculine.

COMMENTS: Five genera and 10 species of Protorhyphidae are known from the Triassic to Late Jurassic-Early Cretaceous deposits of Eurasia. *Vymrhyphus blagoderovi* Krzemiński and Krzemińska, 2003, from the mid-Triassic of France differs from the other two species of the genus by R_{2+3} converging with R_1 and diverging with R_4, *r-m* situated distal to R_4 base, and by the very distal position of the discal cell. Thus, it could be considered as a separate genus.

Brachyrhyphus distortus Blagoderov and Grimaldi, new species figures 7a, 11e

DIAGNOSIS: As for genus.

DESCRIPTION: Measurements: body length (partial) = 3.1 mm, wing length = 1.7 mm. **Wing:** R_1 straight, R_{2+3} slightly sigmoid, converging but not fusing with R_1. R_4 almost straight, very short; length of R_5 $3.5\times$ that of R_4. Section of RS between R_{2+3} and *r-m* about equal to length of *r-m*. Costa continues beyond apex of R_5 at least ½ distance between the apices of R_5 and M_1 (this portion of both wings not completely preserved). Crossveins *r-m* and *tb* near the middle of the discal cell. Crossvein *m-m* connects M_2 and M_3. M stem short, evanescent. Apices of M_1, M_2, M_3, and M_4 almost evenly spaced at wing margin. Distance at wing margin between apices of M_4 and CuA $2\times$ the distance between apices of CuA and CuP.

MATERIAL: Holotype VMNH 2927, ♀.

ETYMOLOGY: The species epithet is from the Latin *distortus*, meaning "distorted", in reference to the distorted proportions of the specimen as a result of fossilization.

COMMENTS: The new genus from the Virginia Triassic is unique among Protorhyphidae in its possession of a very short R_4. A distal shift and reduction of R_4 is common among Bibionomorpha s.l. (*Alinka*, Paraxymyiidae, Eoditomyiidae) and Brachycera, and probably is a result of costalization (see below
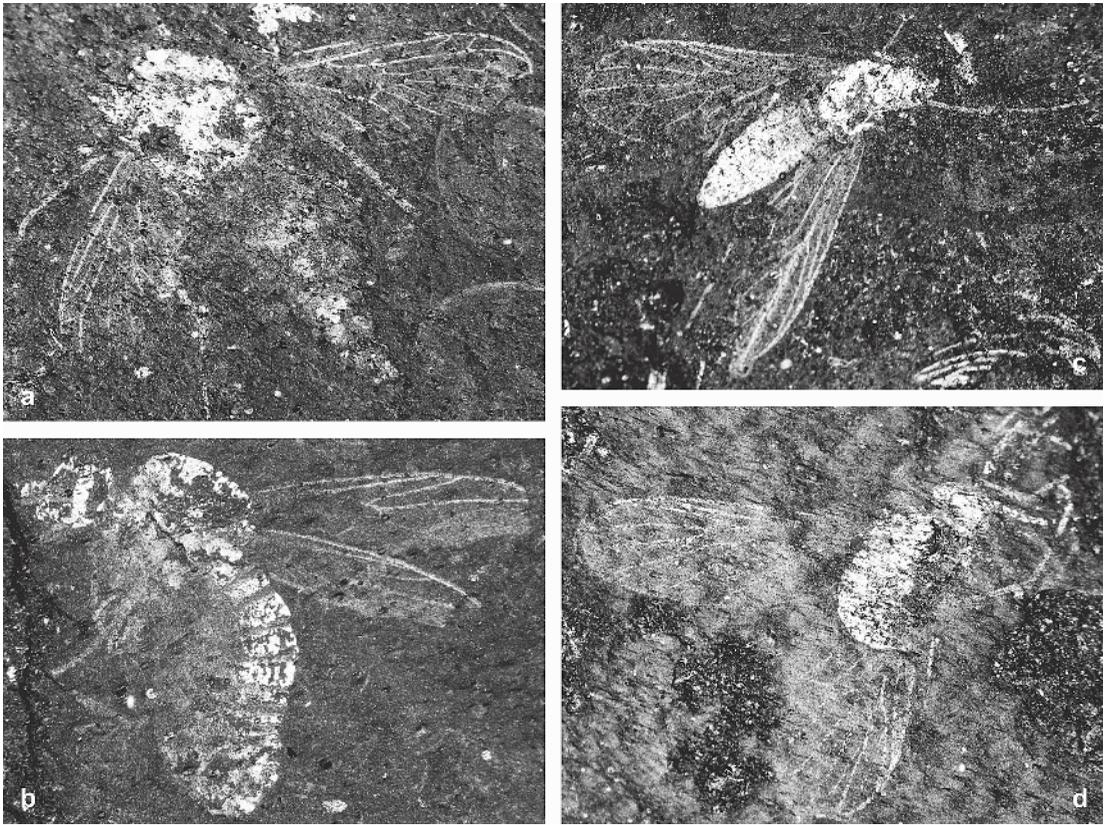
Fig. 7. Photomicrographs of bibionomorphan (a, b) and possible stem-group brachyceran (c, d) Diptera from the Cow Branch Formation. **a.** *Brachyrhyphus distortus* Blagoderov and Grimaldi, holotype VMNH 2927. **b.** *?Crosaphis virginiensis* Blagoderov and Grimaldi, holotype VMNH 797. **c.** *Prosechamyia trimedia* Blagoderov and Grimaldi, holotype VMNH 1371. **d.** *Prosechamyia dimedia* Blagoderov and Grimaldi, VMNH 957. For size scales see fig. 12.

"Phylogeny"). Anisopodidae, which appears to be a sister group or crown-group relative of Protorhyphidae, have lost R_4, thus the new genus demonstrates an intermediate condition between the two families.

FAMILY CROSAPHIDIDAE KOVALEV, 1983

?Crosaphis virginiensis
Blagoderov and Grimaldi, new species
figures 7b, 12a

DIAGNOSIS: Sc short, ends considerably proximal to base of RS; tip of R_1 at level of base of M_{1+2} fork; base of R_{2+3} distal to base of M_{3+4}.

DESCRIPTION: Male. Mesurements: body length = 1.78 mm, wing = 1.36 mm.

Antennae moniliform with 12–13 flagellomeres, flagellomere length nearly equal to the width; scape and pedicel rounded, slightly wider than flagellum. Anterodorsal tubercles may be present on first abdominal tergite. **Wing:** Sc short, its length $0.28\times$ the wing length, meets C well before the base of RS. Sc_2 not apparent. R_4 absent. Base of R_{2+3} distal to the base of M_{3+4}. Stem of M_{1+2} fork at least $2\times$ the length of section of M_{1+2} proximal to *r-m*. Very slight angle in CuA kinked at *m-cu*, apical part of CuA straight. Legs either without or with very short tibial spurs. **Abdomen** broad and short, with hemispheric apical segment, presumably ♂ genital capsule including gonocoxites.
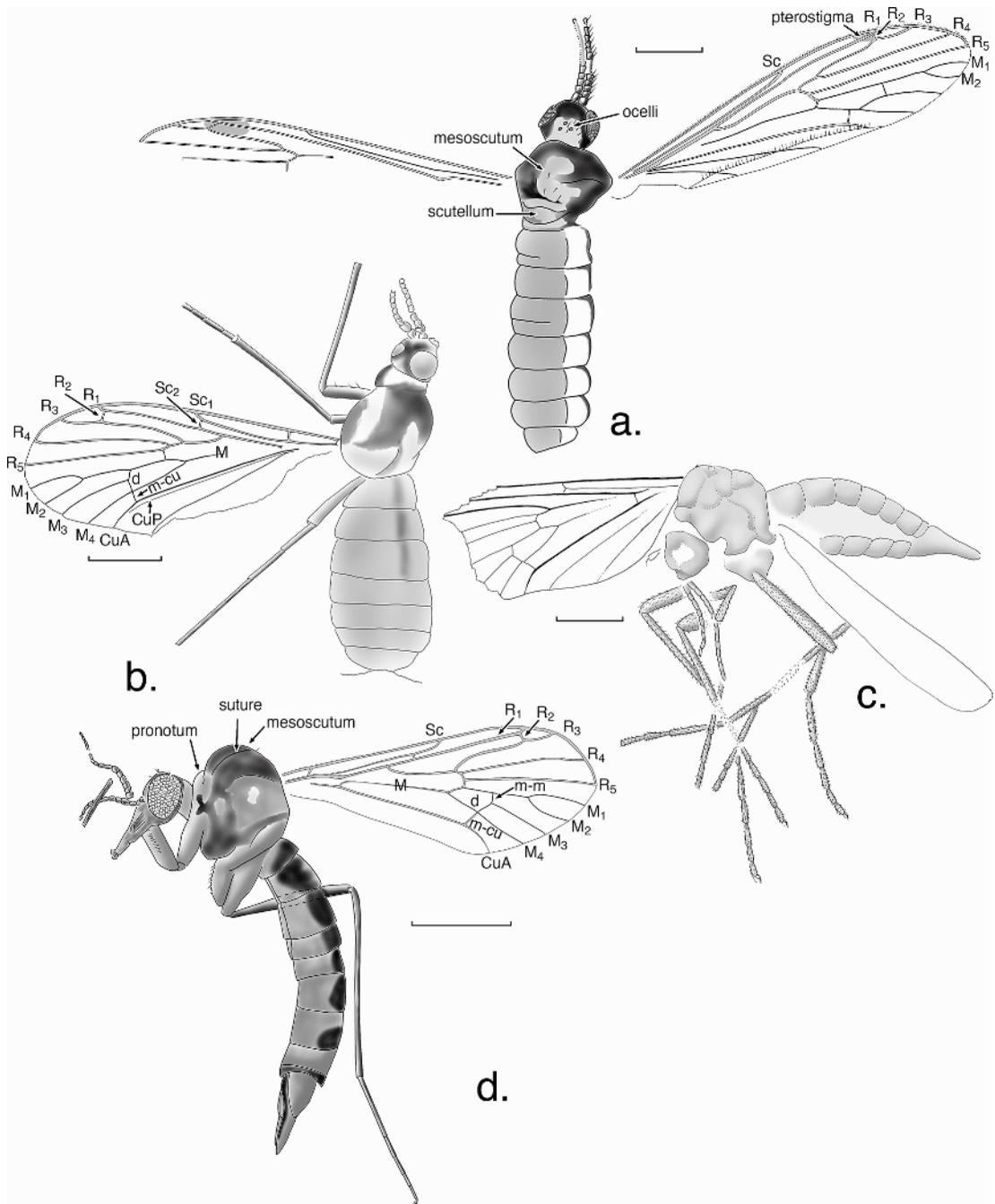
MATERIAL: Holotype VMNH 797, ♂.

Fig. 8. Tipulomorpha from the Solite quarries. **a.** *Architipula youngi* Krzemiński YPM 35986 (Architipulinae) **b.** *Metarchilimonia solita* Blagoderov and Grimaldi, VMNH 3013. **c.** *Metarchilimonia krzeminskorum*, VMNH 3672. **d.** *Metarchilimonia krzeminskorum* Blagoderov and Grimaldi, VMNH 732. Scales = 0.5 mm.
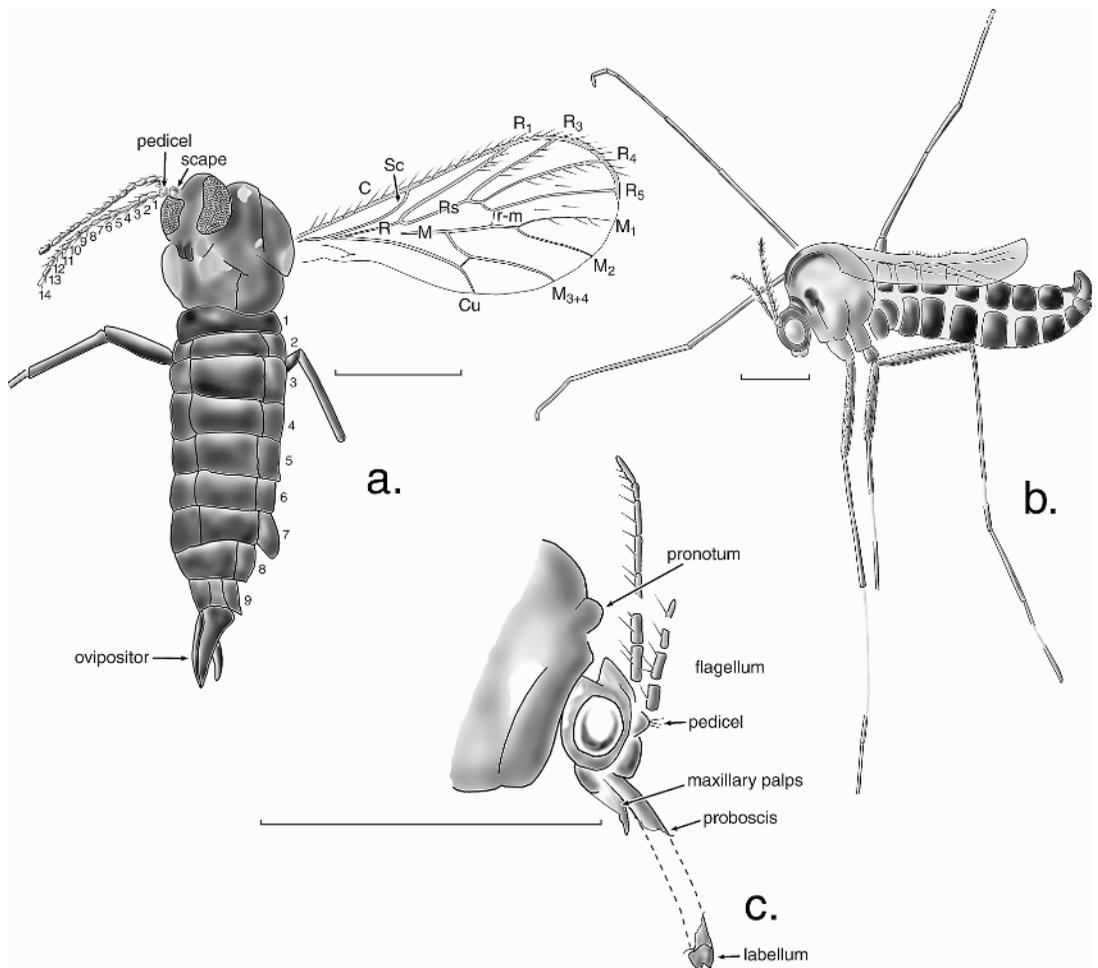
Fig. 9. Psychodomorpha and Culicomorpha from the Solite quarries. **a.** *Triassopsychoda olseni* Blagoderov and Grimaldi (?Psychodidae), VMNH 733. **b.** Culicomorpha (Chironomoidea?), VMNH 951. **c.** Detail of head of culicomorphan VMNH 951 (obverse), showing a long proboscis. Long proboscides in Culicomorpha are generally associated with blood feeding, so this may be the earliest instance of specialization for blood feeding in the fossil record. Scales = 0.5 mm.

ETYMOLOGY: From Virginia, the state of origin of the fossil.

DISCUSSION: *?Crosaphis virginiensis* is smaller than the other described Bibionomorpha from the Solite quarries. It differs from Paraxymyidae by the longer stem of M_{1+2}, which is at least $2\times$ longer than the section of M_{1+2} proximal to *r-m*. R_4 is either absent or not apparent because the apex of the wing is not preserved. The apical part of CuA is almost straight. These features ally this species with *Crosaphis*, and the short coxae, which are smaller than in Sciaroidea, together with short or no apparent tibial spurs, suggest the species belongs in Anisopodoidea.

Incomplete preservation of the type species indicates that this species can only tentatively be assigned to the genus *Crosaphis*. *Crosaphis anomala* Evans, 1956, was described from a single wing impression from the Late Triassic of Australia. After restudying the fossil, V. Kovalev (1983) concluded that it did not belong to Hemiptera, as Evans supposed, but rather was close to mycetobiine Anisopodidae. Restudy of the holotype of *Crosaphis anomala* in the Queensland Museum
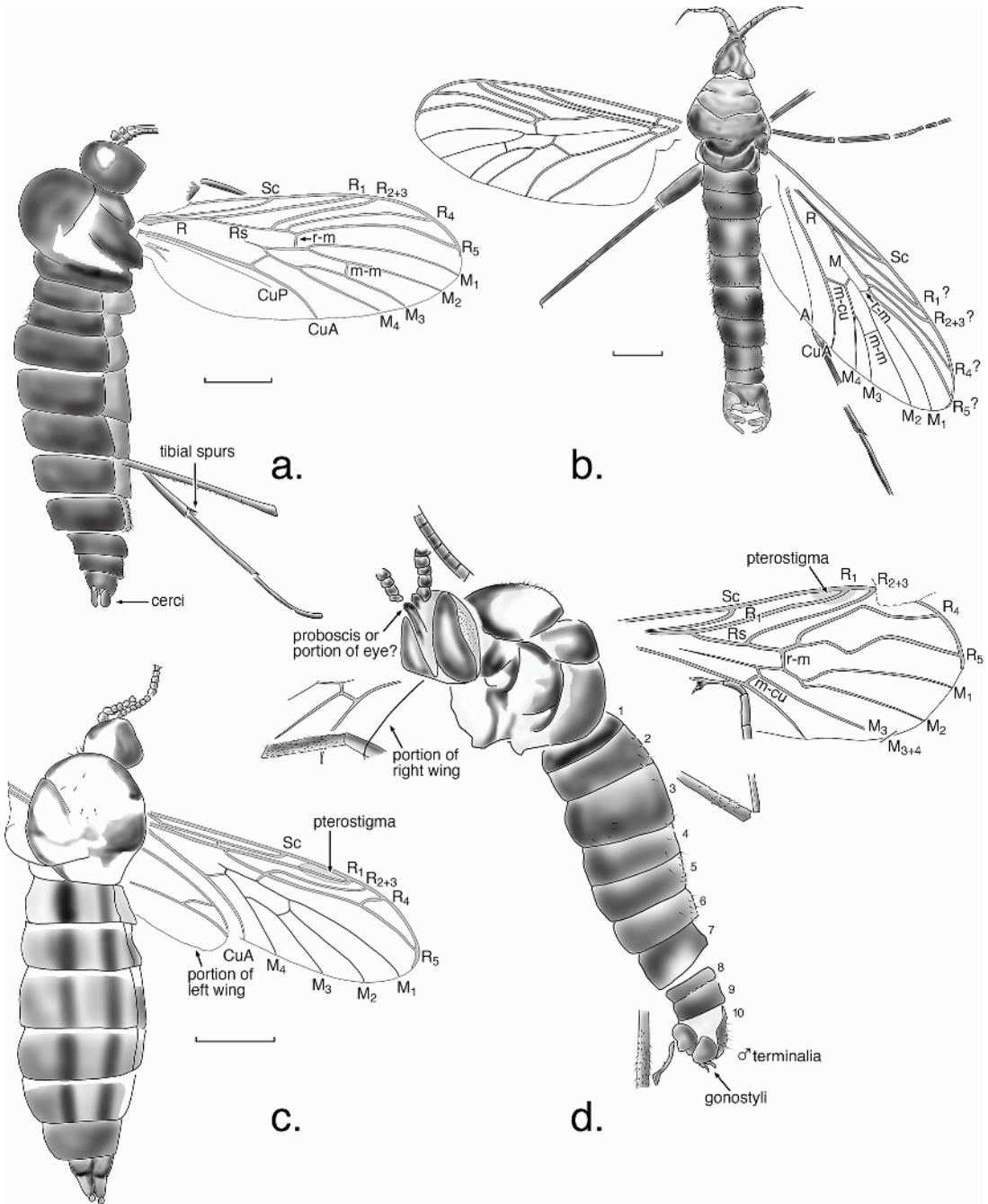
Fig. 10. Bibionomorpha from the Solite quarries. **a.** *Yalea rectimedia* Blagoderov and Grimaldi (Procramptonomyiidae), VMNH 1041. **b.** *Yalea argentata* (Krzemiński) (Procramptonomyiidae), VMNH 3673. **c.** *Alinka cara* Krzemiński (Procramptonomyiidae), YPM. **d.** *Veriplecia rugosa* Blagoderov and Grimaldi (Paraxymyiidae), VMNH 35989.
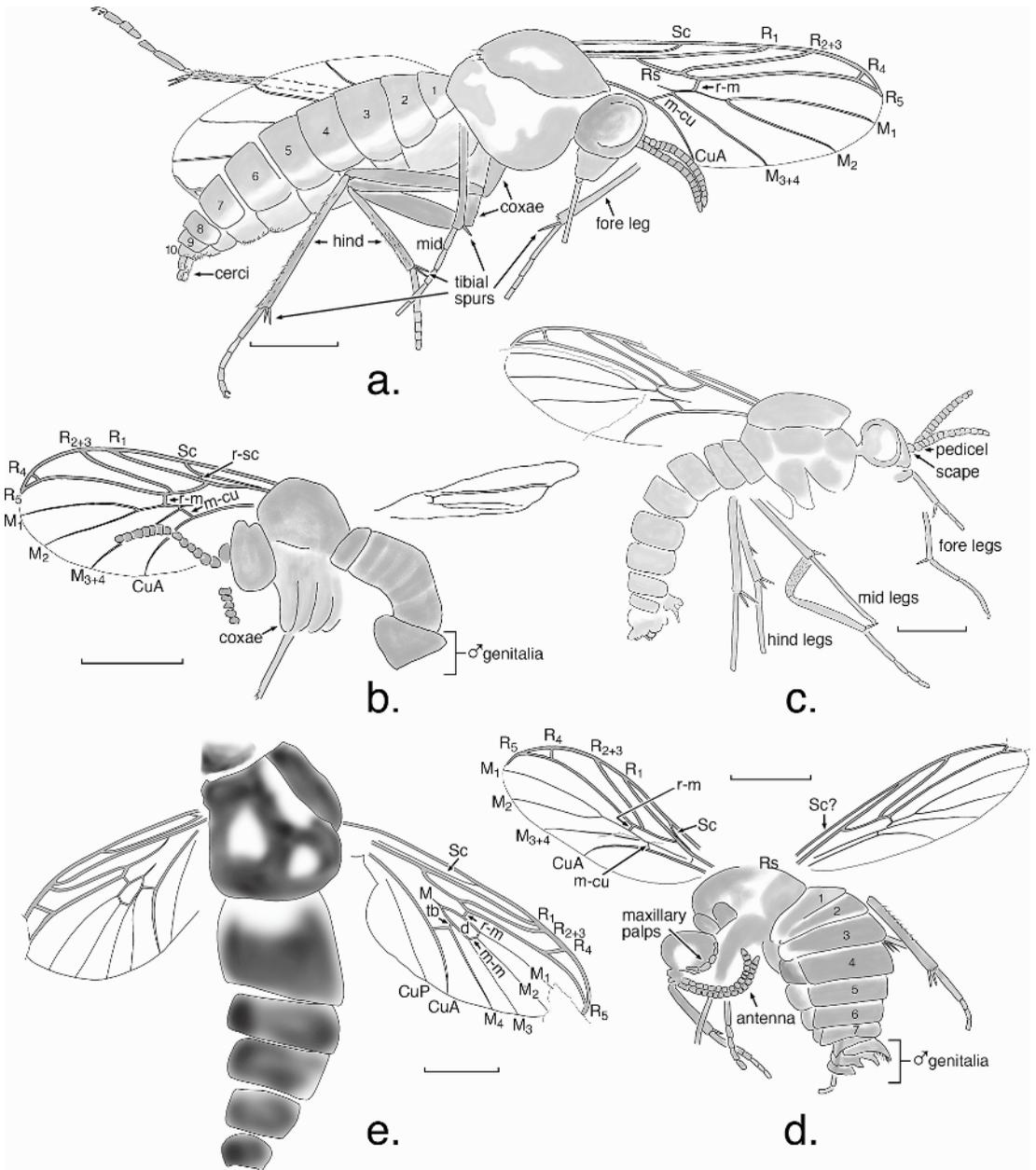
Fig. 11. Bibionomorpha from the Solite quarries. **a.** *Virginiptera certa* Blagoderov and Grimaldi, female, VMNH 731. **b.** *Virginiptera similis* Blagoderov and Grimaldi, VMNH 825. **c.** *Virginiptera certa*, male, VMNH 2998. **d.** *Virginiptera lativentra* Blagoderov and Grimaldi, holotype male, VMNH 2923. **e.** *Brachyrhyphus distortus* Blagoderov and Grimaldi (Protorhyphidae), VMNH 2927. Not to the same scale (scales = 0.5 mm).
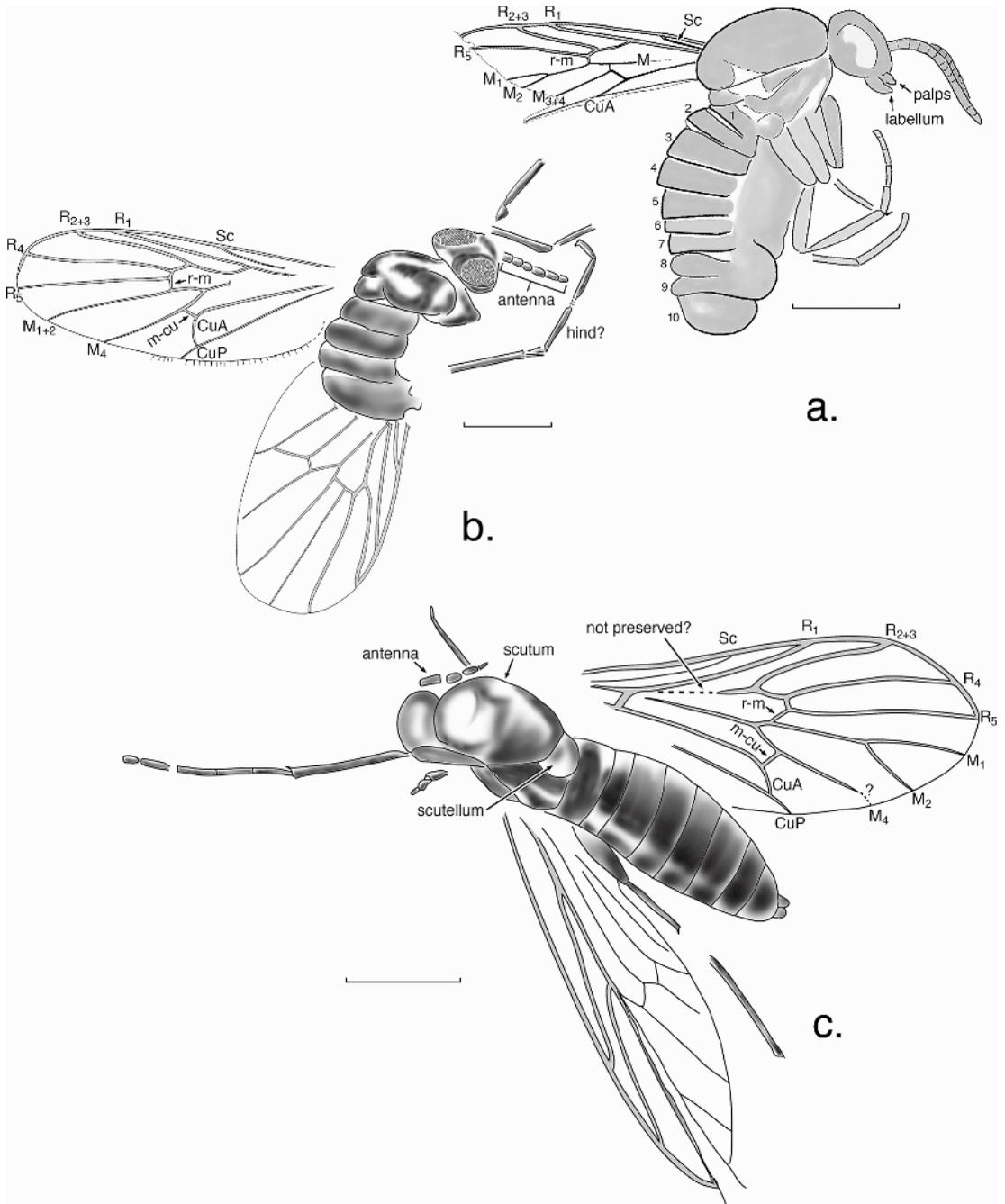
Fig. 12.   Assorted Diptera from the Solite quarries. **a.** ?*Crosaphis virginiensis* Blagoderov and Grimaldi (Crosaphididae: Anisopodoidea). VMNH 797. **b.** *Prosechamyia dimedia* Blagoderov and Grimaldi (Prosechamyiidae), VMNH 957. **c.** *Prosechamyia trimedia* Blagoderov and Grimaldi, VMNH 1371. *Prosechamyia* appears to be an extinct stem group to the large, diverse lineage of flies, the Brachycera. Scales = 0.5 mm.

by one of us (DG) found it to be poorly preserved. Although the presence of parts of the venation were consistent with the venation drawn by Kovalev (1983), much venation was not observable against the rough matrix. It is possible that there may have been some deterioration since Kovalev studied it. Evenhuis (Evenhuis, 1994; Krzemiński and Evenhuis, 2000) doubted the position of *Crosaphis* in Anisopodoidea, on account of the venation that is supposedly similar to that of Bombyliidae mythicomiine. Not only is Late Triassic far too early for a group as recently derived (phylogenetically) as Bombyliidae, but a nearly complete crosaphidid specimen indicates it is not even a brachyceran. Amorim and Tozoni (1994) placed *Crosaphis* in the Mycetobiidae, a living family to which crosaphids are very closely related.

<div style="text-align:center">

STEM-GROUP BRACHYCERA
FAMILY **PROSECHAMYIIDAE**, NEW FAMILY

</div>

DIAGNOSIS: CuA meets CuP well before wing margin and making a closed cell, as in most Brachycera; M_4 lost, as in many Bibionomorpha and some living and extinct "Rhagionidae" s.l. (e.g., *Bolbomyia*, *Palaeobolbomyia*, *Mesobolbomyia*, *Litoleptis*), *m-m* crossvein absent, so there is no discal cell; *r-m* meeting R_5; R_4 and R_5 very long and connected to basal cell; antennae plesiomorphically moniliform.

TYPE GENUS: *Prosechamyia* n.gen.

<div style="text-align:center">

Prosechamyia Blagoderov and Grimaldi, new genus

</div>

DIAGNOSIS: Same as for family.

TYPE SPECIES: *Prosechamyia trimedia* n.sp.

ETYMOLOGY: The genus name is a compound one from the Greek words προσεχής, meaning "bordering" or "adjacent to", and μυία, meaning "fly". The name is feminine.

DISCUSSION: The new genus has a unique combination of characters unknown for any Diptera, living or extinct. The petiolate anal cell is a synapomorphy of virtually all Brachycera (some species, such as *Pseudoernia*, some Rhagionidae and Bombyliidae have CuA and CuP converging but not meeting).

On the other hand, all earliest known Brachycera (Protobrachyceridae, Rhagionidae, Oligophryneidae, and others) have very generalized venation with a discal cell, four branches of vein M, and rather short R_4 and R_5 veins. The new genus has no closed discal cell, no fork of M_{3+4}, very long branches of R_4 and R_5, and moniliform antennae. All living Brachycera, and fossil ones with excellent preservation, have moderately to highly reduced antennae with differentiated antennal segments. Antennae of *Prosechamyia trimedia* are not preserved well enough to determine the number of flagellomeres with certainty, but apical segments are tapered, suggestive of basal Brachycera and resembling the condition observed in *Litoleptis* Chillcott, *Arthroceras* Williston (Rhagionidae), Xylophagidae, and Xylomyiidae. Differentiation of flagellomeres in *P. dimedia* is not preserved. Other synapomorphies of living Brachycera, like posterior elongation of the larval head into the prothorax, vertical movements of larval mandibles, or the reduced number of maxillary palpomeres (from five to two) in adults unfortunately could not be observed in the fossil material.

Prosechamyia definitely is not in Bibionomorpha s.l., some of which have a reduced discal cell and three branches of the radius (e.g., Protopleciidae, Crosaphididae). In those bibionomorphan groups R_{2+3} is usually curved anteriorly and the tips of R_1 and R_{2+3} are close to each other; the base of M_{3+4} is strongly kinked at *m-cu*, suggesting an ancestral state of discal cell structure similar to that of Procramptonomyiidae. The new genus has radial branches almost evenly spaced as in many Brachycera, and M forks symmetrically, similar to Protorhyphidae, Anisopodidae, and many basal Brachycera. The similarity in the wing venation of *Prosechamyia* to the Recent genus *Litoleptis* is especially striking: it differs from the latter by the longer fork of R_4 and R_5, crossvein *r-m* connected directly to R_5 and by the much longer basal cell. Thus, the only synapomorphy of the new genus with true Brachycera is a convergence of CuA and CuP forming a petiolate cell. It is probable that the new genus constitutes an extinct stem group to true Brachycera, having acquired only one of numerous brachyceran synapomorphies.

Caution must be exercised when interpreting relationships—particularly one as dramatic as a sister group to all Brachycera—on the basis of one character. An interesting example of independent evolution of brachyceran characters occurs in some Archizelmiridae, a family of basal Sciaroidea from the Late Jurassic to Late Cretaceous. In one species of this family the antenna is very similar to that in Brachycera, complete with apical flagellomeres modified into a hairlike arista (Grimaldi et al., 2003). If such striking convergence can occur in a relatively complex structure, it seems at least equally probable for there to be convergence in the structure of vein Cu as well.

Prosechamyia trimedia
Blagoderov and Grimaldi, new species
figures 7c, 12c

DIAGNOSIS: Three medial veins, M_1 and M_2 strongly divergent; base of M_{1+2}–M_{3+4} fork at the level of R_{2+3} base; R_4 and R_5 connected directly to basal cell, without a stem; length of *r-m* nearly equal to basal section of M_{1+2}; basal section of M_{3+4} twice the length of basal sections of M_{1+2}.

DESCRIPTION: Measurements: body length 1.9 mm, wing length 1.7 mm. Head round, eyes large. Only four flagellomeres seen, but these are widely separated and presumably some were lost; flagellomeres tapered in width apicad, presumably apical one 1/4 size of most basal preserved one. Sc ends at C at level of base of R_{2+3}. Sc is 0.42× length of wing. R_1 short, 0.58× the wing length. Base of RS apparently not preserved. Crossvein *r-m* oblique, connecting to R_5 near its base. Length of R_{4+5} 2× the length of basal section of R_5 and 1.5× the length of *r-m*. Base of M_{1+2}–M_{3+4} fork at the level of the base of R_{2+3}. Stem of M_{1+2} 1.2× that of M_1, the section distal to *r-m* equal in length to M_1. M_2 widely divergent from M_1. Basal section of M_{3+4} 2× the length of basal section of M_{1+2}. Crossvein *m-m* and vein M_3 absent. M_4 incompletely preserved in unique specimen. CuA forms closed anal cell with CuP, with stem approximately equal to length of *m-cu*. Legs rather long, slender, no tibial spurs visible. Eight visible segments of abdomen, terminalia not apparent, sex unknown.

MATERIAL: Holotype VMNH 1371.

ETYMOLOGY: In reference to the number of medial veins.

Prosechamyia dimedia
Blagoderov and Grimaldi, new species
figures 7d, 12b

DIAGNOSIS: Differs from *P. trimedia* by: vein M_{1+2} simple, not forked; M_{1+2}–M_{3+4} stem proximal to level of R_{2+3} base (vs. at the same level); *r-m* 0.5× the length of basal section of M_{1+2} (vs. nearly equal), and *r-m* transverse (vs. oblique); basal sections of M_{1+2} and M_4 (proximal to *r-m* and *m-cu*) equal in length (vs. basal section of M_4 twice the length).

DESCRIPTION: Measurements: body length 1.7 mm, wing length 1.8 mm. Head and eyes large. Six segments of antenna visible, only slightly tapered to most apically preserved flagellomere. Sc ends at C; its length 0.4× wing length. Length of R_{4+5} 2× that of basal section of R_5 and 1.2× the length of *r-m*. Crossvein *r-m* transverse, veins M_{1+2} and M_{3+4} simple (apparently M_2 and M_3 lost), *m-cu* absent. Basal sections of M_{1+2} and M_{3+4}, proximal to crossveins *r-m* and *m-cu* respectively, are subequal. Tibia (hind) with at least one tibial spur, slightly longer than tibial diameter. End of abdomen curled ventrally; sex unknown, but probably male.

MATERIAL: Holotype VMNH 957.

ETYMOLOGY: In reference to the number of medial veins.

DISCUSSION

PHYLOGENY

This study is an attempt to determine the phylogenetic placement of early fossils of the order Diptera; it is not intended to be the definitive solution to the poorly understood relationships among nematocerous flies. Nematoceran phylogeny has proven problematic thus far, and there is significant disagreement among the major studies. Disagreement may be due to the fact that most of these studies have been based on certain character systems; alternatively, the major lineages may have arisen contemporaneously or nearly so

(and so relationships would be difficult to decipher). Many studies, for example, hypothesize that Tipulomorpha is the sister group to the rest of the Diptera (Hennig, 1954, 1973; Wood and Borkent, 1989; Michelsen, 1996), but one major study hypothesizes that the Tipulidae is much more recently derived and very closely related to the Brachycera (Oosterbroek and Courtney, 1995). Several studies have been largely or wholly relegated to characters of immatures (Wood and Borkent, 1989; Sinclair, 1992); or to particular areas of the adult body, such as the cervical region (Michelsen, 1996) or venation, particularly of fossils (Krzemiński and Krzemińska, 2003; Shcherbakov et al., 1995). Phylogenetic hypotheses by Hennig (1954, 1973) and Oosterbroek and Courtney (1995) were based on immatures and adults. Oddly, there is no comprehensive study of nematoceran relationships based on DNA sequences, and the only one that has been done was based on one gene and minimal taxon sampling (Friedrich and Tautz, 1997). Other DNA studies, mentioned below, have focused on particular infraorders or families. A serious caveat of DNA studies, of course, is that they cannot incorporate fossil DNA, and so they must incorporate morphological structures of living and fossil species to understand the placement of extinct taxa. No study has incorporated many morphological characters of living and extinct Diptera.

We examined the phylogeny of living and extinct Diptera using the morphology of 75 exemplar taxa, representing 45 Mesozoic genera and 30 basal genera of living families of nematocerous Diptera, and two basal families of living Brachycera (Xylomyidae and Xylophagidae). Eighty morphological characters were studied, which represented most major body structures but also included external and internal genitalia of both sexes. Of the 80 morphological characters, 37 (46%) of them were based on wing structure, shape, and venation, which is essential for interpreting Triassic fossil Diptera since most of these taxa are wholly or largely defined by venation. Of the 6,000 cells in the data matrix, 1,891 (31%) of them were not scored or were considered ambiguous because of sexual dimorphism or incomplete preservation of fossils. Most of these unscored cells were characters 30–74 and pertain to minute structures on the body that are generally obscured in compression fossil insects. Most characters were coded for just two states (0, plesiomorphic; 1, apomorphic), but 11 characters with two or more apomorphic states were also scored. With the exception of character 80, all states were nonadditive. The phylogenetic program NONA (Goloboff, 1999) was used, employing the parsimony ratchet with 200 iterations (10 trees per iteration), which generated 264 most-parsimonious trees (MPTs) of length 324, CI 30, RI 72. Figure 13 is the strict consensus of these MPTs, which is some 51 steps longer (L 375, CI 26, RI 66). As expected with a consensus tree, there is less resolution than in the MPTs, in this case primarily among the basal Bibionomorpha. Otherwise, the relationships within the other infraorders and major taxa are well resolved in the consensus tree.

Tipulomorpha in the present study is the sister group to the remaining Diptera, as is traditionally hypothesized (e.g., Hennig, 1954, 1973; Wood and Borkent, 1989), and there is a significant grade of extinct taxa in this infraorder from the Triassic to the present. The infraorder typically includes just the Tipulidae s.l. (or Tipulidae s.s, Cylindrotomidae s.s., and Limoniidae s.s.), though sometimes the winter crane flies, family Trichoceridae, are also included (e.g., Oosterbroek and Courtney, 1995). Typical breeding sites of tipulids are the sediments of shallow streams and ponds, and organically rich mud and wet soils; trichocerids breed in decayed wood. Tipulidae s.l. is the largest family of Diptera with approximately 14,000 described species.

Blephariceromorpha in this study is represented by only one Recent taxon (*Edwarsina*: Blephariceridae) and a primitive Jurassic genus, *Ansorgius*. Deuterophlebiidae is another Recent family in the group, and monophyly of the infraorder is essentially certain. The odd, neotenic family Nymphomyiidae is related either to these (Oosterbroek and Courtney, 1995; Wood and Borkent, 1989) or it belongs to the Culicomorpha (Courtney, 1994). This infraorder, which is the smallest one (approximately 100 species worldwide), is

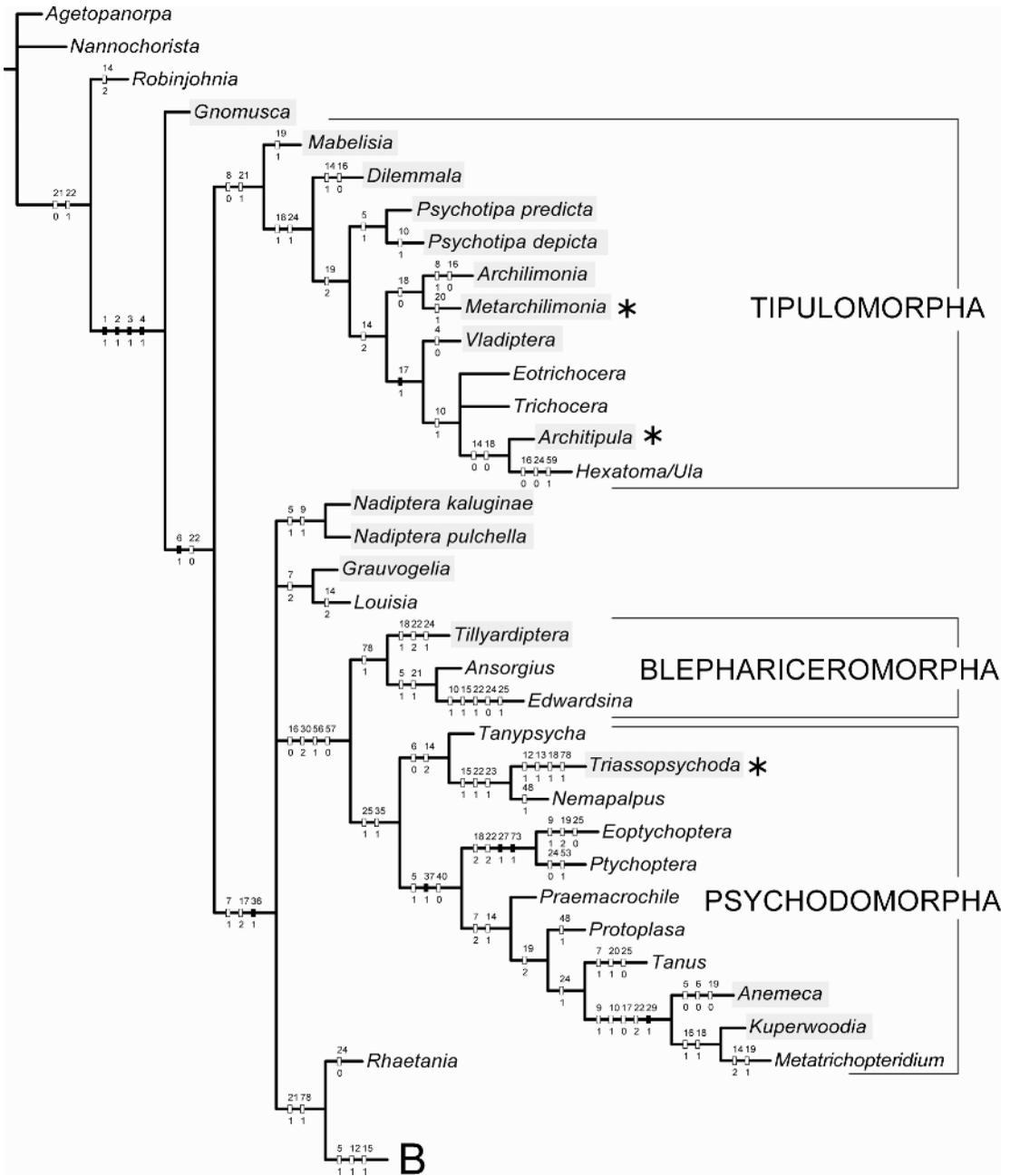Fig. 13. Strict consensus tree (L 375, CI 26, RI 66) of 264 most-parsimonious trees, based on 80 morphological characters of 75 exemplar genera of Diptera (45 of them Mesozoic; see tables 2, 3). Shaded taxa are from the Triassic (others are later Mesozoic and Cenozoic); those with an asterisk are from the Solite quarries. Major infraorders of the Diptera appeared by the Late Triassic.
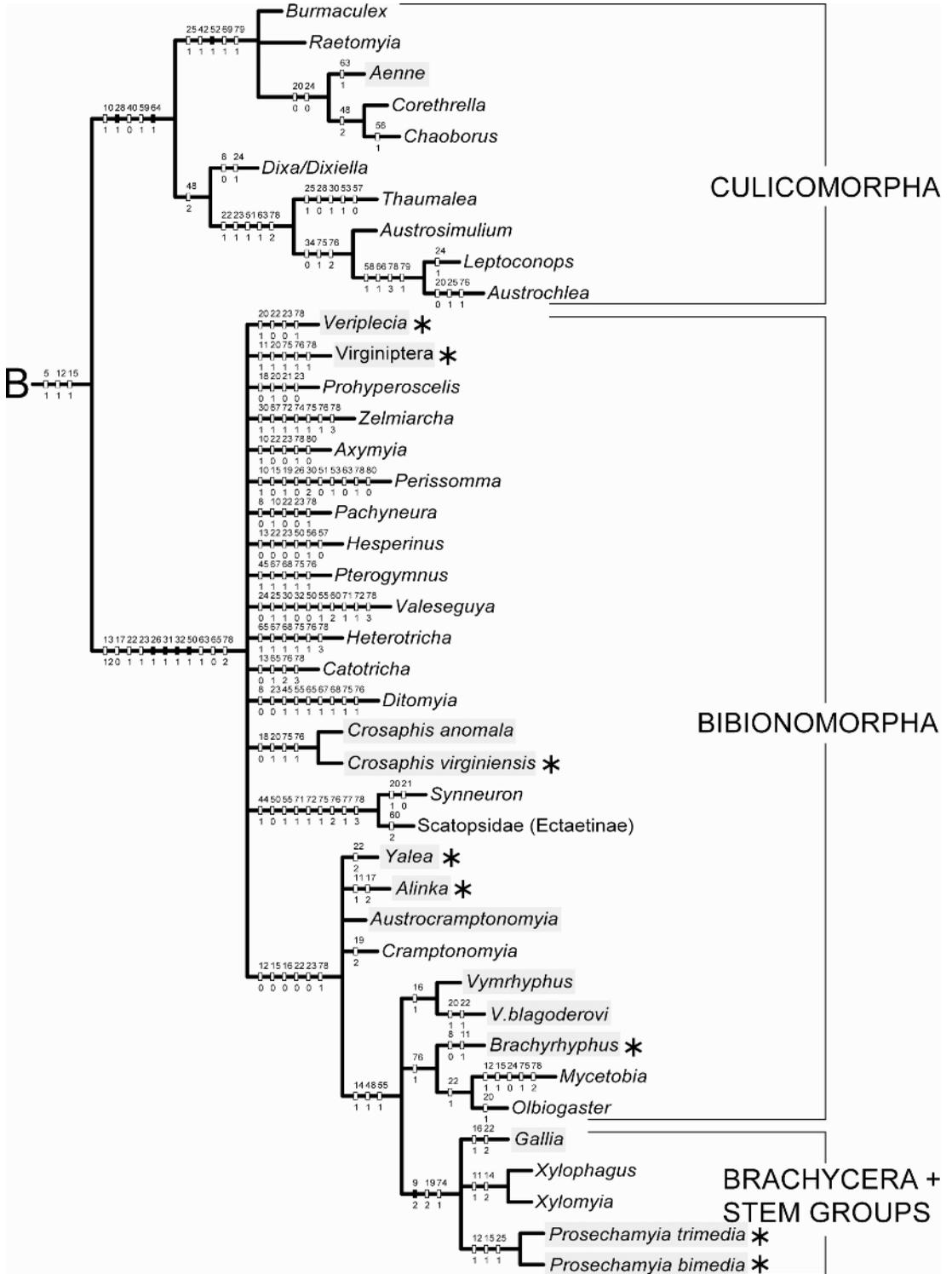
Fig. 13.   Continued

TABLE 2
Character Matrix of Select Mesozoic and Recent Basal Diptera (A = 01, B = 02; see table 3 for characters)

	1 1234567890	1111111 1234567	112 890	22 12	222 345	2222 6789	333333 012345	3333 6789	444444 012345	444 678	4 9	5555555555 0123456789	6666666666 0123456789	7777777778 0123456789
Agetopanorpa	0000000100	0000000	000	12	120	0000	------	--00	-00-0?	000	-	-------?--	------0---	--00000---
Robinjohnia	0000000100	0002000	000	01	000	0000	------	---0	------	-00	-	-------?--	------0---	----0000--
Nannochorista	0000000100	0000010	000	12	020	0000	000000	0000	000000	000	0	0200112100	0000-11000	0000000000
Vladiptera	1110010000	0002011	120	10	010	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Dilemmala	1110--000	0001000	100	10	010	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Psychotipa	1111110000	0000010	120	10	010	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Psychotipadepicta	1111110001	-000010	120	10	010	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Archilimonia	1111010100	0002000	020	10	010	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Mabelisia	1110010000	0000010	010	10	020	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Architipula	1111010001	-000011	020	10	010	0000	------	---0	-00---	000	-	-------?00	------0---	----0-----
Metarchilimonia	1111010000	0002010	021	10	01A	0000	------	---0	-00---	000	-	-------?0-	------0---	----0-----
Gnomusca	1111000100	0000010	001	01	000	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Grauvogelia	1111012100	0000012	001	00	020	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Louisia	1111012100	0002012	001	00	020	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Nadipterakaluginae	1111111110	0000012	001	00	020	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Nadipterapulchella	1111111110	0000012	000	00	020	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Tanus	1111111100	0001002	021	00	010	0000	------	-1--	------	--0	-	-------?--	------0---	----0-----
Kuperwoodia	1111112111	-001010	120	02	011	0001	------	---0	------	--0	-	-------?--	------0---	----0-----
Anemeca	1111002111	-001000	000	02	011	0001	------	---0	------	--0	-	-------?--	------0---	----0-----
Tillyardiptera	1111011100	0000002	100	02	010	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Rhaetania	1111011100	0001012	001	10	000	0000	------	---0	------	--0	-	-------?--	------0---	----0-----
Triassopsychoda	11100-1-2	011-1-2	1-1	01	121	0000	-----1	--00	-12---	-00	-	-------20-	------0--1	----0-----
Aenne	11-10-1-2	-10-1-2	0-0	10	001	0010	------	---0	------	--0	-	-------?--	------1---	----0-----
Yalea	1111111101	0010000	100	12	020	1000	------	--00	-0?---	-00	-	-------20-	------1---	----0-----
Alinka	1111111100	1010002	100	10	020	1000	------	--00	-0?---	-00	-	-------20-	------1---	----0-----
Austrocramptonomyia	1111111100	0010000	100	10	020	1000	------	---0	------	--0	-	-------?--	------1---	----0-----
Vymrhyphus	1111111100	0001010	000	10	020	1000	------	---1	------	--1	-	-------?--	------1---	----0-----
Vblagoderovi	1111111100	0001010	001	11	020	1000	------	---1	------	--1	-	-------?--	------1---	----0-----
Brachyrhyphus	111111-000	1011000	000	10	020	1000	------	---1	-0?---	--1	-	-------20-	-----01010	--01010---
Veriplecia	111111-100	011-1-0	1-1	10	020	1000	------	---0	-0?---	--0	-	-------20-	------0010	---00010--
Virginiptera	111111-1-0	112-1-0	1-1	11	120	1000	------	--00	-0?---	--0	1	-------20-	------11010	--11010---
Crosaphisanomala	111111-100	-11-1-0	0-1	11	120	1000	------	----	------	--?	-	-------?--	------1102-	---1102---
Crosaphisvirgin	111111-1-0	-11-1-0	0-1	11	120	1000	------	--00	-0?---	-??	1	-------20-	------11020	--11020---
Gallia	111111-120	0001010	020	12	000	1000	------	--00	-??---	--1	-	-------?--	------1---	----0001?-
Prosechamyiatrimedia	111111-120	010-1-0	1-0	10	001	1000	------	--01	-0?---	-01	-	-------20-	------1---	-100010---

TABLE 2
(Continued)

	1 1234567890	1111111 1234567	112 890	22 12	222 345	2222 6789	333333 012345	3333 6789	444444 012345	444 678	4 9	5555555555 0123456789	6666666666 0123456789	7777777778 0123456789
Prosechamyiadimedia	111111-120	010-1-0	1-0	10	001	1000	------	--0?	--0?--	-01	-	-------?0-	---1------	---100010-
Eoptychoptera	1111111110	0000002	221	02	020	0100	------	-100	-00---	000	1	--00---?0-	0000??1???	?001000000
Ansorgius	1111111100	0000002	000	10	020	0000	-----0	?000	-10?0-	100	-	--------?00	--0-------	----00010-
Praemacrochile	1111112100	0001002	000	0B	021	0000	------	-?0-	------	--0	1	--0----?--	--0----?--	----00010-
Eotrichocera	1111010001	-002011	120	12	010	0000	------	----	------	--0	1	------?---	--0-------	----0000--
Rhaetomyia	111111-101	-10-1-2	0-1	10	021	0010	------	----	------	--0	-	------?--	--0-------	----0000--
Metatrichopteridium	1111112111	-002010	110	02	011	0001	------	----	------	--0	-	------?---	--0-------	----0001--
Tanypsycha	111100-100	0002002	001	00	021	0000	------	----	------	--0	-	------?---	--0-------	----0000--
Prohyperoscelis	1111111100	-12-1-0	0-1	01	020	1000	------	----	------	--0	-	--0--?---	--1-------	----0002--
Zelmiarcha	1111111100	-12-1-0	1-0	11	120	--00	1110-0	1000	-0000?	000	1	1?001---100	0010000100	0101110302
Ptychoptera	1111111100	0000002	200	02	001	0100	200011	1100	000000	000	1	0001112000	0000011000	0010000000
Edwardsina	1111111101	-0001-2	0-0	11	001	0000	200010	?000	110000	100	0	0100011000	0100?11000	0000000100
Protoplasa	1111112100	0001002	020	00	021	0000	200111	?100	000000	001	0	0000111001	0000011000	0000000000
HexatomaUla	1111010001	-00000A	020	12	000	0000	000111	0000	100000	000	0	0200110101	0000011000	1000000000
Axymyia	1111111101	-11-1-0	1-0	10	020	1000	011010	1000	100000	000	1	1200107100	0001000000	0000000100
Trichocera	1111010001	-002011	120	12	010	0000	100110	0000	100000	000	1	0200107100	0000010000	1000000000
Perissomma	1111111101	-12-010	110	11	120	0000	211010	1000	100000	000	1	1001100100	0000000000	0000000100
Symneuron	1111111100	-12-1-0	0-1	01	120	1000	211010	1000	100010	000	1	0200117100	0001000000	0110121302
ScatopsidaeEctaetinae	1111111100	-12-1-0	2-0	11	120	-000	111010	100A	100010	000	1	0200117100	2001000000	0110121302
Nemapalpus	1111001100	00021-2	0-1	01	121	0000	200011	1000	101110	001	1	0?00117001	0000011001	0000000000
DixaDixiella	1111111001	-10?1-2	121	10	010	0010	000011	1010	000000	002	1	0200100101	0000?10000	0000000101
Corethrella	1111111101	-10-1-2	0-0	10	001	0010	000000	1010	001000	002	1	0210000111	0001?1001	0000000111
Chaoborus	1111111101	-10-1-2	0-0	10	001	0010	000000	1010	001000	002	1	0210001111	0000101001	0000000111
Thaumalea	1111111101	-10?1-2	2-1	11	121	0000	100011	1010	000000	002	1	0210010111	0001110000	0000000201
Austrosimulium	1111111101	-10?1-2	2-1	11	120	0-10	000001	1010	000000	002	1	0101010101	0001110000	0000121201
Leptoconops	11111111-1	-10?1-1	1-1	11	110	0-10	00000A	1010	001000	002	1	0100101111	0001111000	0000121311
Pachyneura	1111111001	-11?1-0	1-0	10	020	1000	011010	1000	100000	000	1	1200107100	0001010000	0000000102
Cramptonomyia	1111111100	0010000	120	10	020	1000	011010	1000	100000	000	1	1200107100	0001020000	0000000102
Hesperinus	1111111100	-10?1-B	1-0	10	02?	1000	011010	1000	10000A	000	1	0200101000	0001020000	0000000202
Mycetobia	1111111100	-11-1-0	2-0	11	000	1000	111010	1000	100010	011	1	1200110100	0001000000	0000110202
Olbiogaster	1111111100	0001000	201	11	020	1000	111010	1000	100010	011	1	1200110100	0001000000	0000010102
Pterogymnus	1111111100	-12-1-0	1-0	11	120	1000	011010	1000	100001	000	1	1200107100	0001020110	0000110202
Burmaculex	1111111101	-10-1-2	0-1	10	021	0010	?---11	1000	?01000	00?	1	0?101?-10-	0000111001	000000001?
Valeseguya	1111111100	-12-1-0	1-0	11	101	-000	110010	1000	100000	000	1	0200117100	2001000000	0110000030?
Austrochlea	111111110?	?10-1-2	0-0	11	121	-010	??2001	1010	?0?000	002	1	0?00101111	0001111000	0000110311

closely related to the Psychodomorpha in our analysis. Larvae live on rocks in shallow, cold, swift streams, especially near waterfalls.

The infraorder **Psychodomorpha** has been one of the most problematic of all major lineages in the Diptera. It typically contains the family of moth flies, Psychodidae (Michelsen, 1996; Oosterbroek and Courtney, 1995), but some authors also include in this infraorder the phantom crane flies (Ptychopteridae) and Tanyderidae (Hennig, 1973; this study), as well as the blephariceromorphs (Hennig, 1973). Wood and Borkent (1989) included in this infraorder the Psychodidae, Trichoceridae, Perissommatidae, Anisopodidae, and Scatopsoidea. Psychodidae and Scatopsoidea breed in wet, foul substrates.

Culicomorpha is the least problematic of the major infraorders, since there is good consensus on the monophyly, composition, and relationships (Hennig, 1954, 1973; Wood and Borkent, 1989; Oosterbroek and Courtney, 1995; Miller et al., 1997; Pawlowski et al., 1997). Our results likewise indicate a monophyletic Culicomorpha, but relationships differ slightly with the other major studies, perhaps because of minimal sampling in this study. *Aenne*, which is known from the Triassic of Britain (Krzemiński and Jarzembowski, 1999) to the Cretaceous of Lebanon (in amber), belongs to the Chironomidae, so in the cladogram in figure 13 it should be the sister group to the other chironomid, which is the very basal living genus *Austrochlea*. Culicomorphan larvae are essentially aquatic, and the ancestral diet of adult females is insect hemolymph and/or vertebrate blood (Grimaldi and Engel, 2005). An undetermined culicomorphan from the Solite quarries reported here has a long proboscis, which is suggestive of its use in sucking blood. As such, it would be the oldest known example among insects of a structure specialized for blood feeding.

Bibionomorpha is a large, complex infraorder whose monophyly is well supported in this study, though internal relationships are poorly resolved. Better resolution is indicated by some studies, such as the close relation of *Valeseguya* (Valeseguyidae) to the Scatopsoidea (Scatopsidae + Synneuridae; Amorim and Grimaldi, 2006). Relationships

TABLE 2
(Continued)

	1234567890	1111111 1234567	112 890	22 12	222 345	2222 6789	333333 012345	3333 6789	444444 012345	444 678	4 9	5555555555 0123456789	666666666 0123456789	77777777778 0123456789
Heterotricha	1111111100	?11-1-0	1-0	11	120	-000	021010	1000	100000?	000	1	1?00010?100	0001010110	0000010302
Catotricha	1111111100	?10-1-0	1-0	11	120	-000	021010	1000	?00000?	000	1	1?00010?100	0001010000	0000020302
Ditomyia	1111111000	-11-1-B	1-0	11	020	1000	011010	1000	100001	000	1	1200010100	0001010110	0000110202
Xylophagus	1111111120	1002000	120	10	020	1000	311010	1001	100000	001	1	0200011?100	1001000000	00001000102
Xylomyia	1111111120	1002000	120	10	020	1000	311010	1001	100000	001	1	0200011?100	1001000000	00001000102

TABLE 3
Characters Used in Phylogenetic Analysis of Select Mesozoic and Recent Basal Diptera[a]

1. Branches of vein Sc: (0) two or more, (1) one.
2. Base of vein R: (0) straight, (1) kinked.
3. Veins M_5 and CuA: (0) fused, (1) separated.
4. Vein A_2: (0) visible, (1) reduced or lost.
5. Allular incision on wing: (0) absent, (1) present.
6. Anal lobe of wing: (0) absent, (1) present.
7. Shape of vein 1A: (0) reaching wing margin distal to cu-a, (1) reduced, not reaching wing margin, (2) reaching wing margin proximally to *cu-a* (anal loop).
8. Apex of vein CuP: (0) in distal half, (1) in basal half.
9. Veins CuP and CuA: (0) parallel or slightly divergent or convergent, (1) strongly divergent, (2) convergent, forms anal cell.
10. Branching of vein RS: (0) $R_{2+3}+R_{4+5}$, (1) $R_{2+3+4}+R_5$.
11. Fork of vein R_{4+5}: (0) long, (1) shorter than its stem.
12. Vein M_{3+4}: (0) forked, (1) M_3 lost.
13. Base of vein MP (M_1 section): (0) developed, (1) vestigial, (2) lost.
14. Vein *m-cu* joins: (0) M_{3+4}, (1) M_4, short stalk between discal cell and *m-cu*, (2) M_{3+4} fork base.
15. Vein *im*: (0) present, (1) absent.
16. Vein *im* joining: (0) M_2, (1) M_{1+2} or base of fork.
17. M forking: (0) symmetrically, (1) discal cell anterior of M stem, (2) discal cell posterior of M stem.
18. CuA distad of *m-cu*: (0) rather straight, (1) kinked and strongly curved posteriorly, (2) straight or curved anteriorly.
19. Vein *r-m* joining discal cell: (0) at the middle of discal cell, (1) distally, (2) proximally.
20. Base of discal cell: (0) proximal to CuP apex or at the same level, (1) distal.
21. Section RS_1 length: (0) at least $3 \times x$ the length of R base, (1) less than $2 \times$ the R base.
22. Sc length: (0) about $0.5 \times$ the wing length, (1) shorter than $0.4 \times$, (2) longer than $0.6 \times$.
23. CuP: (0) complete, (1) reduced, not meeting wing margin.
24. Bases of veins *r-m* and *m-cu*: (0) at same level, line connecting them almost vertically, (1) *r-m* proximad, (2) *m-cu* proximad.
25. Base of vein R_5: (0) oblique or horizontal, (1) vertical, aligned with *r-m*.
26. Tip of vein R_3: (0) tips of R_1, R_3, R_4 and R_5 evenly spaced, (1) R_3 closer to R_1 rather than R_4.
27. Relief of vein CuP: (0) convex for entire length, (1) strongly convex distally.
28. Radial cells: (0) same width, (1) cell R_5/M_1 wider than R_4/R_5, parallel-sided.
29. Vein R_5: (0) normal, (1) continues to the base of wing as a fold.
30. Meron: (0) contiguous with coxa 2, (1) associated with epimeron 2, (2) fused with epm 2 to meropleurite, (3) inconspicuous.
31. Precervical sclerite: (0) absent, (1) present.
32. Laterocervical sclerite: (0) contacts proepisternum, (1) contacts episternal lobe.
33. Laterocervical sclerite: (0) without orifice, (1) with orifice.
34. Mandibles: (0) present and usually better developed or only functional in female, (1) absent.
35. Ocelli: (0) present, (1) absent.
36. Arolium (0): present, (1) replaced with empodium.
37. Last tarsomere of male: (1) normal, not prehensile, (1) capable of folding against penultimate tarsomere.
38. Pedicel: (0) normal, (1) enlarged.
39. Flagellomeres: (0) 10-14, (1) fewer than 8.
40. Parameres: (0) separate, (1) fused to each other.
41. Claws:(0) normal, not folding, (1) fold against distitarsus.
42. Length of setae on flagellomeres: (0) short, (1) as long as flagellomere.
43. Antennal scoids: (0) absent, (1) present.
44. Movemement of gonostyli: (0) horizontal, (1) vertical.
45. Aedeagus: (0) tubular, (1) flattened.
46. Middle legs: (0) normal, (1) shortest of the three pairs.
47. Dorsolateral tubercles on tergite 1: (0) absent, (1) present.
48. MA (arculus): (0) slightly sclerotized, mostly as a crease, (1) as a strong vein.
49. Antepronotum and proepisternum: (0) antepronotum much larger than proepisternum, (1) antepronotum about the size of proepisternum.
50. Basalar pit: (0) absent, (1) present.
51. Postcervical sclerite: (0) normal, (1) produced mesoventrally or absent.

TABLE 3
(*Continued*)

52. Posterior margin of wing: (0) with setae, (1) with scales.
53. Transepimeral suture: (0) present, (1) absent.
54. Coronal suture: (0) present, (1) absent.
55. Ninth sternite of male: (0) well developed, (1) reduced to apodemes.
56. Spermathecal ducts: (0) open separately, (1) with common openings, (2) partly fused.
57. Subalifer: (0) present, (1) absent.
58. Distribution of setae on flagellomeres: (0) irregular, (1) in whorls.
59. Ocelli: (0) present, (1) vestigial or absent.
60. Maxillary palp: (0) 3–5 segments, (1) 2 segments, (2) 1 segment, (3) lost.
61. Wings: (0) normal, (1) dehiscent.
62. Wing position at rest: (0) along the body, (1) over and away from body.
63. Costa: (0) circumambient, (1) abbreviated between tips of veins R_5 and M_1.
64. Empodium: (0) pulvilliform, (1) setiform.
65. Pulvilli: (0) present, (1) absent.
66. Clypeus: (0) small, anterior margin flat or rounded, (1) long and pointed.
67. Coxae: (0) short, (1) as long as thorax height or longer.
68. Tibial spurs: (0) short or absent, (1) several times longer than tibial diameter.
69. Setulae on wing veins: (0) short, (1) long.
70. Male cerci: (0) present, (1) absent.
71. Mesothorax vestiture setae: (0) present, (1) mesothorax devoid of macrosetae.
72. Katepisternum: (0) vertical, (1) extended posteriorly, mesopleural suture kinked.
73. Prehalter: (0) absent, (1) present.
74. Flagellomere specialization: (0) flagellomeres moniliform or clavate, (1) flagellum shortened and apical part forms arista or style.
75. Vein distribution: (0) even through membrane, (1) radial veins condensed with costa.
76. Vein thickness: (0) even, (1) medial veins weakened, (2) medial and cubital veins weakened.
77. Length of radial veins: (0) continue to the tip of the wing, (1) not approaching the tip of the wing.
78. Number of radial branches: (0) 5, (1) 4, (2) 3, (3) 2.
79. Setae on flagellomeres: (0) short, (1) male antennae plumose.
80. Hair plates: (0) absent, (1) radial and axillary, (2) radial and anal (Rohdendorf, 1946).

[a]Character 80 is additive; the rest are nonadditive.

among the Sciaroidea (fungus gnats and allies) have been well treated (Chandler, 2002; Jaschhof, 2001; Jaschhof and Didham, 2002; Blagoderov and Grimaldi, 2004; Hippa and Vilkamaa, 2005; Vilkamaa and Hippa, 2004), and *Veriplecia* and *Virginiptera* (Paraxymyiidae: Late Triassic to Cretaceous) appear to be the basal members of the infraorder. Interestingly, the larval biology of Bibionomorpha is unique among nematocerous flies, in that they are largely terrestrial like the large, monophyletic group, the Brachycera (bibionomorphans, however, feed primarily on fungal matter; most basal brachyceran larvae are predaceous). Several studies (i.e., Hennig, 1973), including this one, break with Wood and Borkent (1989) and Oosterbroek and Courtney (1995) in including Anisopodidae in the Bibionomorpha. In fact, it

appears that Anisopodidae is probably the sister group to the Brachycera, thus rendering the Bibionomorpha paraphyletic. Anisopodidae is represented in the Triassic by *Vymrhyphus*, and fossils of the family become more diverse through the later Mesozoic.

Brachycera is the largest and most diverse infraorder in the Diptera, with 110 families and probably over 100,000 described species. It is a definitively monophyletic group as based on, among other features: (1) larval features (obviously not preserved in fossils); (2) reduction of the antennal flagellum to eight or fewer segments (commonly four or fewer), and significant differentiation of the flagellomeres; (3) reduction of the maxillary palp to 1–2 segments; (4) veins CuA and CuP (often interpreted as CuA_2 and A_1) with their apices meeting before the wing margin (forming
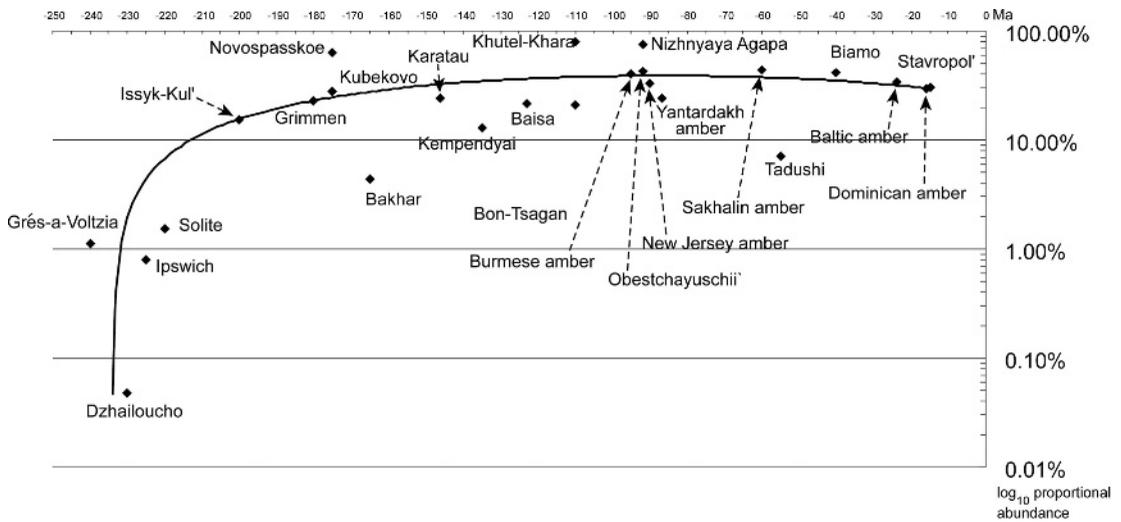
Fig. 14. Relative abundance of Diptera through time, as measured by $\log_{10}$ proportion of Diptera specimens among total number of fossil insect specimens from representative, significant deposits (see table 4). Dipteran abundance asymptotes toward modern levels in the Jurassic because of diversification within infraorders.

a closed cell) or nearly so. Fusion of veins R_2 and R_3 (Hennig, 1973) has been suggested as a fourth defining character, but this is widespread among nematocerous flies. *Gallia*, from the mid-Triassic of France, is known only from the wing, and it has been classified as a brachyceran (Krzemiński and Krzemińska, 2003). This is based, however, just on wing venation. Our discovery of *Prosechamyia* from the Solite quarries reveals an additional Triassic fly with convergent Cu veins, but the antennae (albeit incomplete) are filiform, indicating *Prosechamyia* is a stem group to true Brachycera. Thus, in lieu of antennal and other structures of *Gallia*, it is quite possible that it too is a stem group to true brachycerans.

DIPTERA ABUNDANCE AND DIVERSITY IN THE TRIASSIC

Our results indicate that stem-group and even some derived members of most major dipteran infraorders existed by the Late Triassic. Diptera, however, were rare in the Triassic, which contrasts starkly with their abundance later in the Mesozoic (fig. 14). For example, in the Triassic deposits at Dzhailoucho (Kyrgyzstan, Central Asia) only

11 fly specimens were found among approximately 20,000 insects; in the Ipswich Series of Australia only four out of 500 (Anderson and Anderson, 1993); and at Grés-a-Voltzia in France only 59 adults out of 5,300 other insects (Krzemiński and Krzemińska, 2003; Marchal-Papier et al., 2000). In the Early Jurassic of Germany—some 40 million years later—Diptera comprised approximately 23% of all insect specimens, second only to Hemiptera (26%) (Ansorge, 1996); and in the Late Jurassic of the spectacular insect Concentrat Lagerstätte of Karatau, Kazakhstan, Diptera comprised 24% (4,791 of 19,879) of all insect specimens (www.palaeoentomolog.ru). By the Early Cretaceous, Diptera comprised approximately 21% of all insect specimens, such as in the diverse deposits at Baissa, Siberia. These proportions of course reflect biases in the preservation of lacustrine and marine littoral deposits, but the Cretaceous and Tertiary abundance of Diptera is also apparent in amber from those periods, with Diptera (particularly Chironomidae and Ceratopogonidae) typically being the most abundant insect order in amber (e.g., Rasnitsyn and Quicke, 2002; Grimaldi, 2000; Grimaldi et al., 2002).

TABLE 4
Abundance of Diptera in Major Deposits of Fossil Insects from the Triassic to Neogene
(C, compression; A, amber)

Locality	Age	%	Insects (N)	Diptera (N)	Taphonomy	Reference
Grés-a-Voltzia	−240	1.11%	5300	59	C	Krzemiński, 2003, Papier et al., 2000
Dzhailoucho	−230	0.05%	23332	11	C	www.palaeoentomolog.ru
Ipswich	−225	0.80%	500	4	C	www.palaeoentomolog.ru
Solite	−220	1.52%	3300	50	C	
Issyk-Kul'	−200	15.23%	2836	432	C	www.palaeoentomolog.ru
Grimmen	−180	22.67%	1200	272	C	Ansorge, 1996
Novospasskoe	−175	63.26%	3100	1961	C	Kalugina, Kovalev, 1985
Kubekovo	−175	28.18%	1022	288	C	www.palaeoentomolog.ru
Bakhar	−165	4.35%	5421	236	C	www.palaeoentomolog.ru
Karatau	−146	24.10%	19879	4791	C	www.palaeoentomolog.ru
Kempendyai	−135	12.94%	1182	153	C	www.palaeoentomolog.ru
Baissa	−123	21.25%	24476	5200	C	www.palaeoentomolog.ru
Bon-Tsagan	−110	21.12%	9959	2103	C	www.palaeoentomolog.ru
Khutel-Khara	−110	80.01%	3331	2665	C	Sontag, 2003
Myanmar	−95	40.17%	3012	1210	A	Grimaldi et al., 2002
Obestchayuschii	−92	42.85%	1202	515	C	www.palaeoentomolog.ru
Nizhnyaya Agapa	−92	75.10%	257	193	A	www.palaeoentomolog.ru
New Jersey	−90	33.46%	1052	352	A	Grimaldi et al., 2000
Yantardakh	−87	23.89%	854	204	A	www.palaeoentomolog.ru
Sakhalin	−60	43.41%	940	408	A	Zherikhin, 1978
Tadushi	−55	7.16%	3843	275	C	www.palaeoentomolog.ru
Baltic	−40	41.44%	7111	2947	A	www.palaeoentomolog.ru
Biamo	−24	34.17%	1718	587	C	www.palaeoentomolog.ru
Dominican Rep.	−16	29.65%	11814	3503	A	D.Grimaldi, unpubl.
Stavropol'	−15	30.53%	3449	1053	C	www.palaeoentomolog.ru

Diptera from the Triassic of Virginia comprise some 1.5% of all insect specimens, which is comparable in abundance to other Triassic deposits. Overall, the trend indicates that Diptera were rare in the Triassic, comprising approximately 1% of all insects and dramatically increasing in abundance in the latest Triassic to earliest Jurassic. By the Late Jurassic ~150 Ma the abundance of Diptera nearly reached that of the Tertiary level, and remained there. By the end of the Triassic flies were global. All Diptera from the locality that has yielded the oldest such specimens, the Grés-a-Voltzia sandstones, belong to extinct and the most basal lineages. Indeed, most basal families (Vladipteridae, Archilimoniidae, Grauvogeliidae, Nadipteridae) occur in Europe and Central Asia. A virtual absence of Diptera in the Australian Triassic is possibly a sampling problem, but insects from the Newcastle Formation in Belmont, Australia are very distinctive among what are otherwise globally uniform Permian insect faunas, so the Australian Triassic Diptera could reflect regional differences (Ponomarenko and Sukacheva, 1998). There has been little change in the tectonic position of Australia during those 30 Ma between the Triassic and Permian deposits.

In conclusion, the Diptera evolved from a Late Permian *Permotipula* or *Robinjohnia*-like ancestor that had saprophagous immatures and adults. The exact timing is difficult to discern since the Early Triassic is virtually unknown for insects, but we hypothesize that true, two-winged Diptera originated in the earliest Triassic ca. 245 Ma. By 20 Ma after the Permo-Triassic boundary, stem groups and some derived members of the major infraorders had appeared. This would suggest a very rapid diversification or radiation of Diptera in the Early Triassic, which could be the basis for why relationships among infraorders and other higher lineages of living nematocerous flies appear to be so obscure.

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