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Triassic Diptera and initial radiation of the order

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New Triassic Diptera Nematocera from Central Asia are described: *Mabelysia charlesi* (Limoniidae), *Gnomusca molecula* and *G. renyxa* (?Limoniidae, Gnomuscinae subfam. n.), *Vymrhyphus tuomikoskii* and *V. triassicus* (Protorhyphidae, Anisopodoidea), *Nadiptera kaluginae* and *N. pulchella* (Nadipteridae fam. n., Ptychopteroidea), *Vladiptera kovalevi*, *Dilemmala specula*, *Psychotipa predicta*, and *P. depicta* (all Vladipteroidea superfam. n. and Vladipteridae fam. n., two latter Psychotipinae subfam. n.), *Kuperwoodia benefica* and *Anemeca liya* (both Hennigmatoidea superfam. n. and Hennigmatidae fam. n., the former Kuperwoodiinae subfam. n.). The type of the latter family, *Hennigma cladistorum*, is described from the Cretaceous of Mongolia, and *Nadiptera anachrona* from the Jurassic of Kyrgyzstan. Mesozoic Eoptychopteridae are divided into three subfamilies. The Jurassic family Ansorgiidae is transferred into Blephariceroidea; Triassic Alinkidae is provisionally assigned to Pachyneuroidea. The most primitive dipterans, Vladipteridae, are placed in Tipulomorpha. The radiation of Nematocera is discussed (original phylochronogram and modified system given); some infraordinal concepts are criticized. The origin of Diptera from Permian Mecoptera similar to Robinjohniidae is suggested; it's hypothesized that the dipteran wing structure was formed mainly due to transfer of mecopteran hindwing characters onto the forewing.

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Key words: Triassic Diptera, initial radiation, Central Asia.

Contents

To the memory of our colleagues,
Nadezhda S. Kalugina and Vladimir
G. Kovalev

Introduction

The oldest Diptera are known from the Triassic beds of Australia (Kovalev, 1983b), North America (Krzeminski, 1992c), Mallorca and France (see below), and Central Asia. These latter, represented by the isolated wings only, were already discussed (Kovalev, 1984, 1987, 1989; Kalugina & Kovalev, 1985), some of them even schematically figured (Kovalev, 1983a), but have never been formally described. In most of them, collected at Dzhailoucho locality, the weak veins and especially crossveins are obscured with the uneven surface of sediment, the pigmentation is poorly preserved, and moreover, the real wing proportions might be considerably affected by the distortion of clay matrix. The fossils, now studied in detail, represent the most diverse Triassic dipteran fauna known, and are helpful in testing phylogenetic speculations made by Kovalev and other authorities.

One more Triassic dipteran wing from another locality seems to be very strange at first glance in possessing a supernumerary ('third') anal vein, never reported previously in any dipteran. However, a rudiment of this extra vein could be easily observed in some members of each dipteran infraorder (it was figured, but not interpreted by some authors). The comparative study undertaken by us shows that the construction of wing stalk (basiala) is even more phylogenetically indicative than demonstrated by Rohdendorf (1946, 1951) and Hennig (1968). The basiala characters proved to be useful in allocation of some Triassic wings, which are primitive enough to combine the characteristic plesiomorphies of Tanyderidae (Psychodomorpha) and Tipulomorpha.

The Diptera described by Rohdendorf (1961, 1962) from the non-marine deposits of Kyrgyzstan were considered the Late Triassic, but later the beds were shown to be of Early Jurassic age (Genkina, 1966). All these fossils belong in fact to the families known from the other Jurassic faunas (on fossil 'Archidiptera' see below, under Blephariceromorpha).

Studying fossils, one accepts ancestral (i.e., paraphyletic) taxa as no less natural and legitimate than monophyletic ones (Rasnitsyn, 1988). The Diptera are considered derivatives of Mecoptera. Subdivision of Nematocera into four infraorders (Hennig, 1968) and 17 superfamilies is accepted (for the reasons and details see below); the Asilomorpha are used in the sense of Brachycera Orthorrhapha.

All the new taxa are known only from holotypes, deposited in the Paleontological Institute (PIN) of Russian Academy of Sciences, Moscow.

Triassic faunas of Diptera

The early Middle Triassic (Anisian) Buntsandstein of Mallorca contains rather rich entomofauna (Calafat Colom & Saez Verger, 1987), including a specimen (Calafat Colom, 1988, Foto 23: 'forma alada indeterminada') identifiable as Diptera. Recently numerous undescribed dipteran specimens were reported from the nearly synchronous *Voltzia*-Buntsandstein of Vosges Mts, France (Krzeminska, 1994). These are the oldest dipterans recorded.

Most of the wings described below were collected in the Madygen Formation of South Fergana, Kyrgyzstan (two nearby localities, Dzhailoucho and Madygen), dated as Middle or Late Triassic (Ladinian-Carnian) on paleobotanical data (Dobruskina, 1982). So far as known, the Madygen entomofauna is more rich and diverse in Diptera than the other Triassic ones: 11 specimens treated in this paper represent 11 separate species which are classified into 8 family group taxa, 4 of these latter endemic to the Triassic. 7 more specimens remained undescribed due to poor and/or fragmentary preservation.

Two more dipteran wings were found in the Triassic of South (Ketmen' Mts, Koldzat Formation) and East Kazakhstan (Kendyrlik syncline, upper Tologoi Formation), the former locality dated paleobotanically as Ladinian-Carnian and the latter as Late Triassic (Norian-Rhaetian) (ibid.). The species from Ketmen' is congeneric with one from Dzhailoucho, and the genus from Kendyrlik is related to those from Madygen Formation, all belonging to endemic Triassic families.

The dipteran described (first as Homoptera Aphidoidea) from the Late Triassic Ipswich Group of Queensland, Australia (Mt. Crosby; Carnian on paleobotanical data; ibid.) is the only representative of Crosaphididae (Kovalev, 1983b); undescribed Jurassic specimens mentioned as crosaphidids (ibid.; Kalugina & Kovalev, 1985: 18) belong elsewhere, and the status and relationships of the group remain doubtful.

Another quite diverse dipteran assemblage is known from the early Late Triassic Cow Branch Formation of eastern USA (Carnian on paleobotanical data; Olsen et al., 1978). 13 specimens reported belong to extant Limoniidae (7 specimens, including 5 of *Architipula youngi*), Eoptychopteridae (1; other members of the family are of Jurassic and Early Cretaceous age), Procramptonomyiidae (1; others from the Jurassic), endemic Alinkidae (2, both of *Alinka cara*), and uncertain families (2) (Krzeminski, 1992c). Numerous specimens of *Mormolucoides* Hitchcock collected in the beds of similar age (Turners Falls, Mass.) are exuviae of (sub)aquatic larvae, presumably of Diptera (Ponomarenko, 1993: 185); probable dipteran pupae are present in Cow Branch assemblage (determined as '?phyllocarid crustaceans' in Olsen et al., 1978: Fig. 4A).

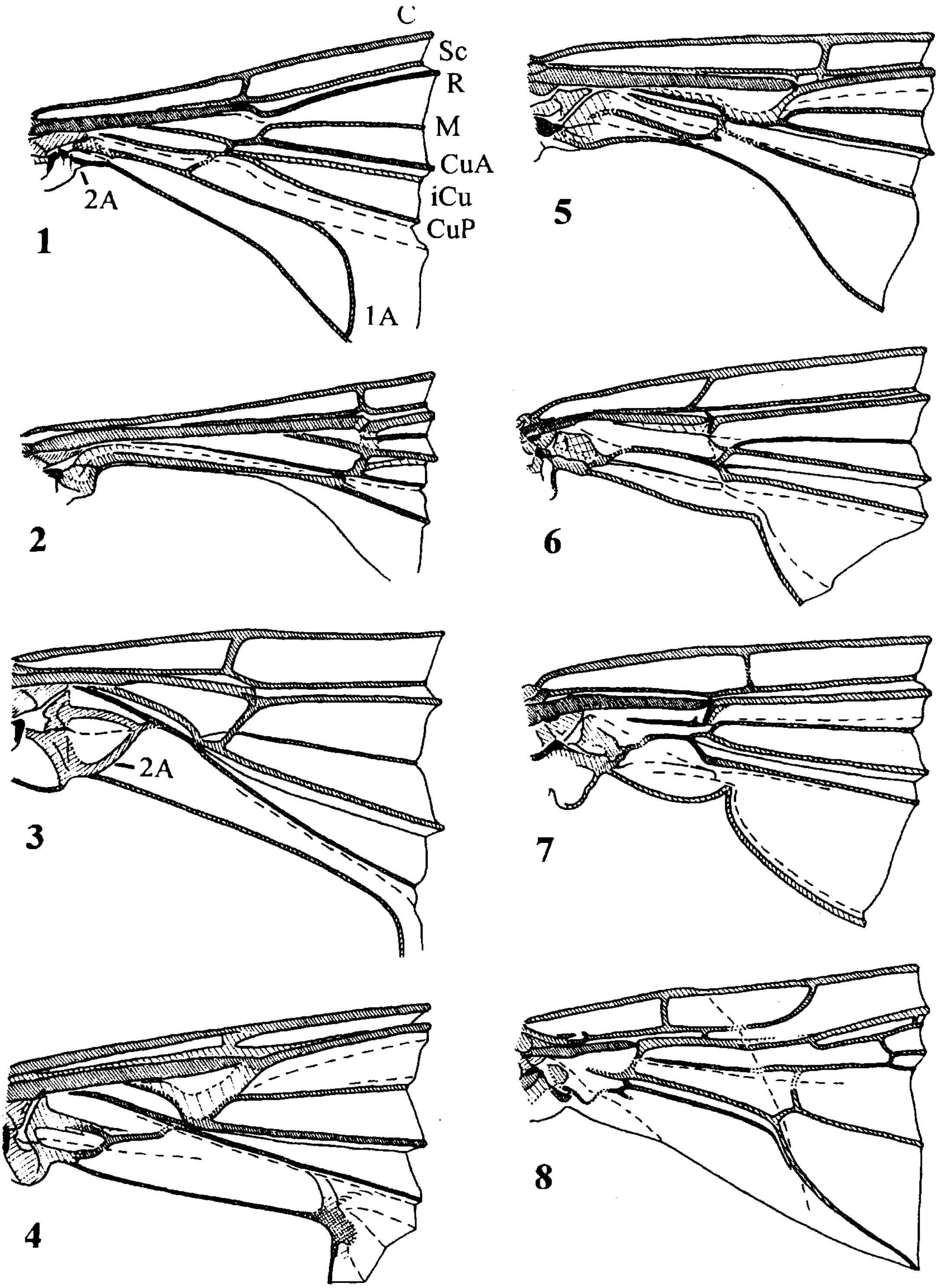
If the data on Asiatic and American assemblages are comparable, the latter containing much lower proportion of genera and families endemic to the Triassic might be younger than judged from paleobotanical data. The supposition is further confirmed by the heteropteran assemblages of these localities. The Cow Branch aquatic Heteroptera include the extant nepomorphan families Notonectidae and Belostomatidae (Olsen et al., 1978: Fig. 3D,E; determined by Yu. A. Popov), unknown from the other Triassic entomofaunas. The abundant water bugs of upper Tologoi Formation belong to primitive Nepomorpha (near extant Corixidae), the remaining Triassic bugs (from presumably older localities) are very rare and belong to extinct families hardly referable to either infraorder (Yu. A. Popov, pers.comm.). Both Diptera and Heteroptera are unknown before the Triassic and recorded through the above faunas as phyletic lineages *in statu nascendi*.

MORPHOLOGY

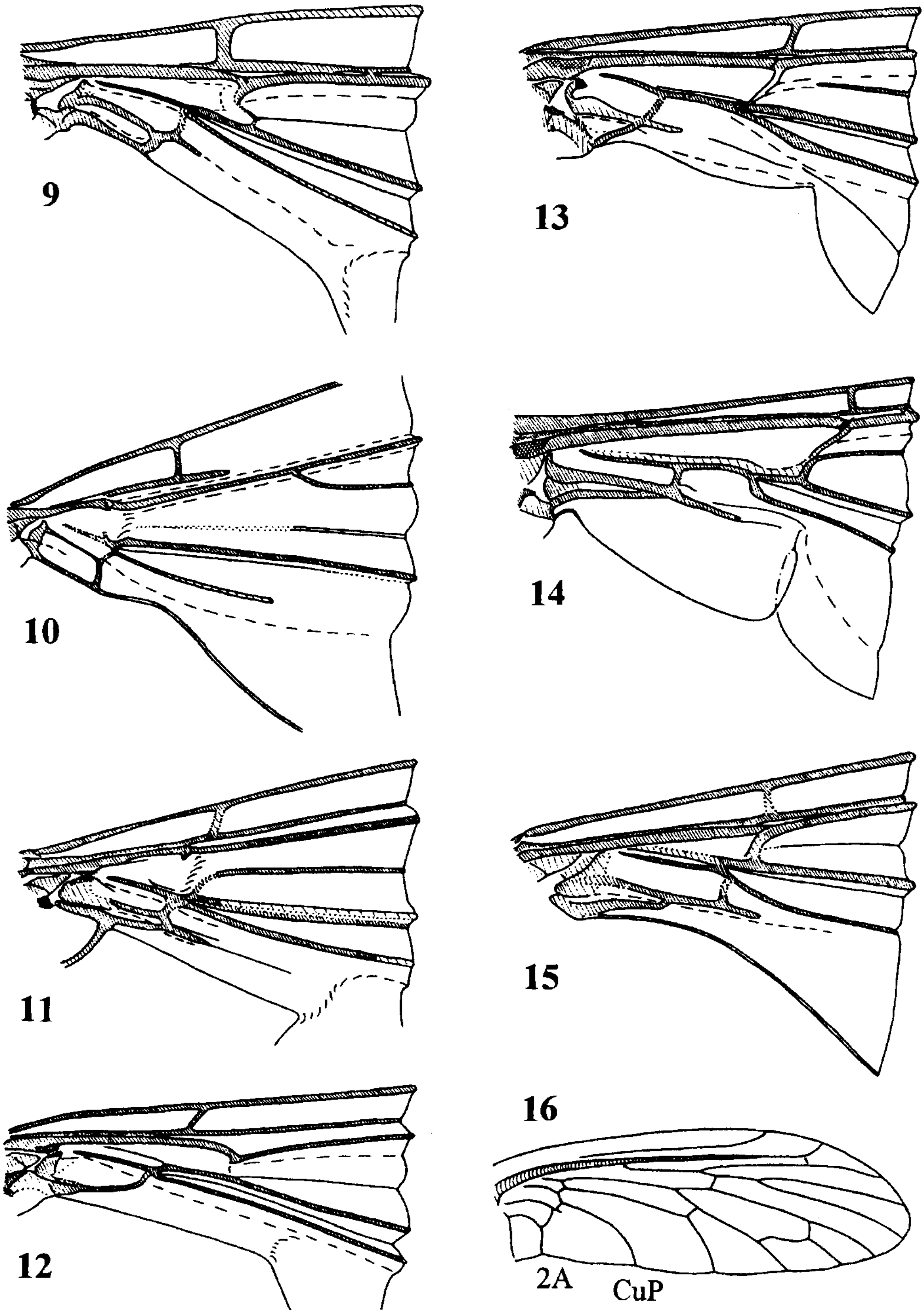
One more vein in dipteran wing

Traditional nomenclature of dipteran wing veins proposed by Tillyard (1919b) designates three veins posterior to CuA as CuP, 1A and 2A. Recently, the alternative, far more plausible interpretation appeared (Wootton & Ennos, 1989): a thickened groove, adjacent to strongly convex **CuA** and not reaching wing margin, is a secondary **pseudovein** not homologous to CuP; the former 1A is actual **CuP**, retaining characteristic concavity in generalized forms (but often turning mostly convex in more derived ones); and the so-called 2A (convex) is the only true anal vein not lost in the Diptera (Figs 1—15).

The above homology could be further modified. The intercubital 'pseudovein' is actually an apomorphy of Diptera, but it seems to be restored rather than appearing *de novo*. The complex CuA (consisting of anterior convex and posterior concave component) could be found also in the hindwings of some primitive Poly- and Oligoneoptera: Blattida, Grylloblattida, Mecoptera (the order ancestral to Diptera), Trichoptera, Megaloptera and Neuroptera (Ponomarenko & Rasnitsyn, 1974; Sukacheva, 1976; Novokshonov, 1992); but CuA is mainly concave in the case due to anterior convex component being weaker and shorter. Hindwing CuA of similar structure is characteristic of various Coleoptera (e.g. Elateridae, Scarabaeidae, Chrysomelidae), turning mainly convex in some instances (e.g. Staphylinidae)



Figs 1—8. Recent Nematocera, basiala.
1, *Trichocera maculipennis* Meigen; **2**, *Tipula fulvipennis* Degeer; **3**, *Protoplasa fitchii* Osten Sacken (Tanyderidae); **4**, *Agathon* sp. (Blephariceridae); **5**, *Ptychoptera contaminata* L.; **6**, *Dixa aestivalis* Meigen; **7**, *Cryophila lapponica* Bergroth (Chaoboridae); **8**, *Thaumalea* sp. Folds in dashed line.



Figs 9—16.

9—14: Recent Diptera, basiala: **9**, *Protaxymyia melanoptera* Mamaev et Krivosheina (Axymyiidae); **10**, *Perissomma congrua* Colless; **11**, *Bolitophila* sp. (Mycetophilidae s.l.); **12**, *Bibio rufipes* Zetterstedt; **13**, *Sylvicola zetterstedti* Edwards (Anisopodidae); **14**, *Rhynchocephalus* sp. (Nemestrinidae). **15**, **16**, Jurassic Eoptychopteridae: **15**, *Proptychopterina yeniseica* Lukashevich (paratype PIN 1255/1507, basiala; Middle Jurassic); **16**, *Crenoptychoptera conspecta* Lukashevich (holotype PIN 1670/403, pupal wing pad; Lower (?) Jurassic; after Lukashevich, in press, a).

Table 1. Changes in nomenclature of some dipteran wing veins

NOMENCLATURE:								
Tillyard 1919b	arculus	R4+5	M	CuA	CuP	1A	2A	—
McAlpine 1981	**MA**	R4+5	M	CuA	CuP	A1	A2	—
Wootton & Ennos 1989	arculus	Rs3+4	M	CuA	pseudovein	**CuP**	1A	—
this paper	MA	R4+5	M	CuA	**iCu**	CuP	1A	**2A**
HOMOLOGY	MA base	**MA**	**MP**	**M5**	**CuA**	CuP	**Pcu**	**1A**
Vein position	+	+	—	+	—	—/+	+	+

("+" - convex, "—" - concave).
Changes of Tillyard's nomenclature accepted herein in **bold**.

and in related Strepsiptera. This condition never has a counterpart in the forewings, except for some Carboniferous Protoptera (the order considered closest to initial Pterygota) and dipterous male scale insects (Homoptera Coccomorpha; see below). According to Rasnitsyn (1980), both CuA and CuP are primitively concave, and the convex position of CuA is caused by its fusion with posteriormost basal branch of M, termed M5 after Tillyard (1926); the convex-concave anterior cubital complex should be interpreted in this way as incompletely fused or secondarily dissociated **M5+CuA**. The free concave CuA s.str. was probably restored in dipteran forewing (along with free MA base) in accordance with hindwing pattern (see below). The above homology is supported by the tracheation of pupal wing in *Tipula* (Byers, 1989): M5 is supplied with the branch of radial trachea, i. e. from anterior tracheal stem, not penetrating posterior to M in other insects (e. g. Lepidoptera; Comstock, 1918).

The only convex vein posterior to M5, preceded by two concave ones, CuA s.str. and CuP, is the **1A** of Comstock and Needham. In generalized insects, this vein is supplied with a separate trachea and never so intimately connected with the 3rd axillary sclerite as following anals, so it was given the status of an independent vein, postcubitus (Pcu) by Snodgrass (1935). The Pcu is more or less reduced distally in most Diptera, except Tipulomorpha.

A basal rudiment of one more distinctly convex vein, not recognized as such previously, is observed in both fossil and recent Diptera studied. It is rather long and free in Triassic *Vladiptera* gen. n. (Fig. 17), becoming shorter in other Tipulomorpha and entering Pcu in other infraorders (for details, see the next section). Obviously, it is true 1A, the only remnant of anal (s.str.) veins preserved in Diptera.

Bearing the proposed homology in mind for comparison with other insect orders, it is nevertheless convenient to follow the traditional nomenclature (as modified by Wootton & Ennos) in taxonomy of Diptera (Table 1, Fig. 1). The abbreviature **iCu** could be used for intercubital 'pseudovein' when necessary, and the newly found anal vein should be designated as **2A**.

The transverse cuticular ridge, connecting the R stem in vicinity of humeral crossvein (*h*) to M stem in most Diptera, was variously interpreted as either the base of free part of M ('arculus'; Tillyard, 1919b), or the secondary outgrowth of R ('phragma'; Rohdendorf, 1951), or (the base of) convex main branch of M (**MA**; McAlpine, 1981). The latter homology seems the most appropriate as judged from the retention of free MA base in hindwings of Megaloptera, Neuroptera (Martynov, 1928: 89), primitive Trichoptera and Mecoptera (Novokshonov, 1992), some Lepidoptera (Brodsky, 1989: Fig. 23), and its presence in forewings of some Neuroptera (Comstock, 1918: Figs 188, 191, 196—198, 205, 211). (Basal brace in coleopteran hindwings is rather free base of M itself than of MA, contrary to Kukalová-Peck & Lawrence, 1993.) Therefore, the posterior branch of Rs (+MA) in Diptera (like in Mecoptera and neuropteroids) corresponds to MA (**R4** = MA1, **R5** = MA2), and M itself to MP.

R2 is retained as free vein in some Psychodomorpha, but reduced to crossvein in most Ptychopteroidea and Tipulomorpha and atrophied in Culicomorpha and Bibionomorpha, as well as in Brachycera; in these latter groups, the three main Rs branches are **R(2+)3**, R4 and R5 (Hennig, 1954; for the reasons discussed below under Axymyiomorpha). In some primitive forms, supernumerary *r-rs* and/or other crossveins are present along with free (Cretaceous *Hennigma* gen. n., Fig. 33) or brace-like R2 (some *Dicranota* spp., Limoniidae), the fact seeming at first glance to confirm the supposition (Wood & Borkent, 1989: 1343) that the single crossvein between R1 and R3 in other Nematocera could be homologous to either *r-rs* or R2. However, all the fossil evidence agrees rather to the hypothesis of Alexander (1927a) on the crossvein being always homologous to R2.

The R5 is more or less distinctly convex through the Diptera, whereas R2-4 and M1-3 almost invariably concave, the fact also supporting its homology with MA2. **R5 convexity** is continued proximad

('MA1 stem' by Séguy, 1959) up to MA base (Culicoidea except Dixidae, most Asilomorpha) or towards it (some Psychodomorpha, Anisopodidae, Pachyneuridae). Sometimes it is shifted posteriad into the *r-m* space (Ptychopteroidea, Syrphidae) and turns vein-like ('vena spuria' of *Ptychoptera* and some Syrphidae; in the latter untracheated but functioning as afferent blood vessel; Arnold, 1964).

Comstock (1918) interpreted the branch posterior to M3 as CuA1 in Diptera, because it is convex like CuA and often appears arising rather from the latter. However, its homology to **M4** (Tillyard, 1926) is correct, because M4 often turns convex in Mecoptera, and CuA fork is lost in all scorpionflies (including presumed ancestors of Diptera), except for the most primitive family Kaltanidae (Novokshonov, 1994a).

On wing deformation and basiala structure

The deformation of insect wing during the stroke cycle is restricted by stiff supporting areas and confined to flexion lines and deformable areas (Wootton, 1981). In Diptera the supporting structures are V-shaped spars, rigid in bending but easily twisted (Ennos, 1989): **costal spar** (C+Sc-R+), **cubital spar** (CuA+iCu-CuP, or in fact M5+CuA-CuP), and sometimes also **medial spar** (R5 convexity with adjacent concave veins). In costalized wings (i.e. with veins shifted towards leading edge) the Rs branches are often incorporated into costal spar (e.g. in Chironomoidea, Sciaroidea=Mycetophiloidea, Scatopsoidea, Stratiomyiidae). The cubital spar is attached to costal one through M base and/or MA. The M stem (and medial spar when present) is hinged at its own base (and MA when developed) allowing wing camber to be reversed under aerodynamic loads; both costal and cubital spars rotate slightly when M hinges up, and medial spar controls camber (ibid.).

The compliance of costal spar depend on the strength and position of crossveins: proximally situated *h* and usually more distal *sc-r* (Sc2 of authors). The latter is variably placed (and often obliterated or lost); the main variants might be conventionally designated as humeral (interstitial with *h*), basal (somewhat distad of *h*), presectoral (before Rs origin), postsectoral, and terminal. Two *sc-r* are recorded in *Hennigma* (Fig. 33) and in some specimens of *Pedicia rivosa* (Limoniidae; in presectoral and terminal positions), therefore the single *sc-r* could be not homologous through the Diptera. (However, the terminal brace in some Syrphidae, e.g. *Eristalis*, is derived from the basal border of pterostigma rather than represents second *sc-r*.) So far as studied the following *sc-r* positions are characteristic of main subdivisions (first recorded for taxa given in **bold**): Trichoceridae — postsectoral; Tipuloidea — presectoral to terminal; **Ptychopteroidea** — humeral to postsectoral; Tanyderidae and Psychodidae — terminal; **Culicoidea** — presectoral; Thaumaleidae — presectoral; **Chironomidae** — humeral (usually absent); **Simuliidae** — humeral or basal (often absent); Cramptonomyiidae, Pachyneuridae and Bibionidae — presectoral; Mycetophilidae s.l. — basal to terminal; **Axymyiidae** — rather basal; **Anisopodidae** — basal (usually absent); Asilomorpha — basal (except rather presectoral in *Solva* and *Lampromyia*).

The **nodal flexion line** (running from Sc apex up to CuP apex in generalized wing, but to CuA apex and often from R1 apex due to strengthening of cubital and costal spars in Diptera) allows the distal wing part to deflect ventrad at the beginning of upstroke; in Tipulidae the line appears to be adapted rather for posterior bending (Wootton & Ennos, 1989). In some (especially broad-winged) Diptera the nodal flexion is pronounced, and concave veins are provided with flexible elements: bend and/or break of Rs; and desclerotization of M, localized before the fork (**thyridium**) or involving the whole stem. This is true of Tipulidae, Tanyderidae, Psychodidae, several Eoptychopteridae, and some Bibionomorpha and Brachycera. Ennos (1989) considered some model brachycerans (along with unrelated Simuliidae — see below) as representing the distinct functional wing type; however, the nodal flexion is more widespread in Nematocera than its distinct structural signs, and was observed e.g. in Trichoceridae and Limoniidae (when manipulating with alive insect). In Psychodidae and Muscomorpha Schizophora the nodal line is shifted to near humeral level (bifurcates anteriorly in the latter group), and subbasal flexion is combined with basal torsion in their wings (as well as in simuliids), probably allowing fast manoeuvres (ibid.).

Due to functional replacement of claval supporting zone characteristic of generalized broad-based forewing (Wootton, 1981) by the cubital spar in Diptera, the whole wing base became narrow and more compliant in torsion. R kink, basal brace series and alular incision mark off the **basiala** (Rohdendorf, 1946: Fig. 30; 1949: 99), or wing stalk (McAlpine, 1981), containing vein bases, from the remaining **wing blade**. Basal brace series comprises crossveins and transverse bases of longitudinal veins: *h*, *sc-r* (when shifted basad), MA (when restored), CuA base (in fact restored basal *m-cu*), *cu-a*, and *ia*. The basal wing torsion is confined to basiala and facilitated by the incompletely sclerotized joint between R stem and basiradiale (Ennos, 1987: Fig. 8).

The R forms a distinct **kink** near *h* (often confined to vertical plane and unconspicuous from above), probably functioning as an additional torsion joint (Brodsky, 1988: Fig. 24; 1989: 27) or as a hinge during camber reversal (Wootton & Ennos, 1989); the section before the kink referred to as R base below. A transverse suture-like constriction could be developed at the kink (often reaching Sc and imitating one more strong *sc-r)*. In Culicomorpha it is transformed into the perfect torsion joint (Figs 6—8; see also SEM photograph by Bocharova-Messner in Sokolov et al., 1979: Fig. 203), so that wing blade could be broken off from (and fossilized without) stalk. The kink is well expressed in horizontal plane and approximated to the symmetrically opposed basal bend of M stem, hinge suture absent, and MA nearly not formed in e.g. Trichoceridae (Fig. 1), some Limoniidae, Cylindrotomidae, Pachyneuridae, and most Sciaroidea. The kink is confined mainly to vertical plane, hinge or joint present, and MA vein-like in e.g. Tipulidae (Fig. 2), Ptychopteridae, Culicomorpha, Anisopodidae, and most Asilomorpha. The degree of kink and MA development varies within all the main dipteran lineages and seems to be roughly correlated with flight abilities; both parallel developments and reductions could be hypothesized, but as judged from fossils the former condition is not secondary at least in some Tipulomorpha.

Strong convex **M base** (i.e. M section prior to junction with CuA, or in fact before M5 separation), running nearer to R base and more or less in alignment with CuA stem, is inherited by Tipulomorpha from Mecoptera (Wootton & Ennos, 1989). In Psychodomorpha the convex M base is nearer to concave Cu base, sometimes (e.g. in *Ptychoptera*; Fig. 5) concealing the latter from above (two veins remain separated by vertical membrane). In Anisopodoidea and Asilomorpha the M base is either lost or represented by rudiment (Fig. 13) or even convex channel vein (Fig. 14) adjacent to concave Cu base. In other Bibionomorpha the M base is usually lost, if traceable then weak, neutral, diverging from R base: Bolitophilinae (Fig. 12), some Mycetophilinae, some Keroplatinae (Matile, 1990: Figs 30, 32), Hesperininae (Hardy, 1981: Fig. 13.8), and Pleciinae (Rohdendorf, 1946: Pl. I, Figs 2—3). In Culicomorpha the M base is weak, concave and adjacent to R base (Dixidae, Fig. 6), or parallel to it (proximally associated with neither R base nor basivenalia, Fig. 7), or lost, whereas the Cu base is often reduced proximally and captured by *cu-a*. Due to elaborated R joint and reduced M and Cu bases the narrow wings of Culicoidea, Chironomidae and Ceratopogonidae are capable of maximal basal torsion (and no nodal flexion, probably except for slight one in Dixidae). In more broad-winged Thaumaleidae (Fig. 8) the pronounced nodal line is shifted proximad, and at least some genera fold their wings along it in repose (McLellan, 1983: Fig. 16). In Simuliidae the wing becomes broadest in the infraorder, and peculiar prehumeral flexion (Ennos, 1989) instead of nodal one is developed.

The improvement of basal torsion in Culicomorpha was undoubtedly connected to increase of stroke frequency: maximal value recorded for the infraorder (above 1000 Hz in *Forcipomyia*) is thrice higher than for Brachycera (370 Hz in *Tachina*), four times than for Bibionomorpha (ca. 250 Hz in *Scatopse*), six times than for Psychodomorpha (165 Hz in *Psychoda*) and eight times than for Tipulomorpha (above 120 Hz in *Pachyrrhina*; Sotavalta, 1947).

The **alular incision** of posterior wing margin is not developed yet in Tipulomorpha, and often poorly indicated in other narrow-winged forms. The wing could be produced as **anal lobe** beyond the incision and as **alula** before it, the latter appearing in few Psychodomorpha (some Eoptychopteridae), in Culicomorpha (usually incipient), in few Bibionomorpha (Anisopodidae), and various Brachycera.

The **CuP**, initially concave due to close association with **claval fold** (Tipulomorpha, Tanyderidae), turns partly or mostly convex: at least proximally in Culico- and Asilomorpha, at least distally in Bibionomorpha, distally in Eoptychopteridae and Ptychopteridae. In two latter families and Anisopodidae the CuP distally diverges backwards from straight claval fold, the latter being adjacent to CuA apically (CuA often sigmoidal beyond *m-cu* in the case) and supporting cubital spar; in most Brachycera the straight CuP is fused with CuA near apex. CuP base tends to be associated with 1A at humeral level, becoming angled towards (some Ptychopteroidea, Culicomorpha and some Asilomorpha) or at least approximated to it (Anisopodidae and other Asilomorpha).

Claval veins, 1A (= Pcu) and 2A, are separated by concave **interanal fold**, which is basally provided with sclerotised ridge (on the underside of the wing) and connected to the distal corner of 3rd axillary sclerite. (Often this dark ridge is much more conspicuous than the paler 1A and 2A, when the wings are studied in microscope slides; see e.g. Pl.IV, Fig.10 in Rohdendorf, 1946.) 1A and 2A are free and enter margin in Tipulomorpha (like in Mecoptera), in most of them 2A being extremely short, *ia* more or less reduced, and interanal fold reaching margin. Among extant taxa the free 2A is best recognizable in Trichoceridae (Fig. 1). In Tipulidae (Fig. 2) and some Limoniidae (with hinge suture and MA formed), the thickened 1A base and bulbous rudiment of 2A are intimately fused, being divided only by interanal ridge (of lower wing surface) entering angulate emargination. In other infraorders the *ia* is strong, and 2A beyond it lost (traceable in pupal wing pads of Eoptychopteridae, Fig. 16), therefore short 2A seems to enter 1A forming anal loop (Figs 3—15; the same way of loop formation is observed in other orders possessing it, e.g. Trichoptera, Hymenoptera, Hemiptera). The interanal fold is subparallel to margin basally, sometimes being continued along 1A. The 1A itself is reduced distally, never reaching margin, in generalized groups traceable at most up to alular incision (usually as colourless channel vein, Fig. 11), or joining Cu base (*cu-a* replaced with anastomosis in Tanyderidae and Blephariceridae, Figs 3—4; sometimes weak distal 1A reaching incision retained, most distinct in *Edwardsina* — Edwards, 1929: Pl. V, Figs 1—2). The reduction of distal 1A is obviously correlated with the development of alular incision (Wood & Borkent, 1989: 1343), and like the latter character is subject to partial reversal. Unlike the initial condition, the 1A beyond alular incision is always blind and concave; it is absent in most (if not all) Psychodomorpha, Axymyiidae, Pachyneuroidea, Bibionidae and Bolitophilinae, fold-like in most Culicomorpha, more or less vein-like in Anisopodoidea and some Mycetophilidae, reaching its maximal development in some Brachycera. The change of positions of both distal CuP (to convex) and distal 1A (to concave) restores the regular corrugation of the wing blade, interrupted with appearance of concave iCu in initial Diptera.

In Bibionomorpha a pair of proprioceptive **hair plates** ('chetaria' of Rohdendorf, 1946; contrary to his opinion, they are sensory, not coupling, structures) (Figs 11—13) is situated at the primary torsion joint (between distal median plate and Cu base; Brodsky, 1988: Fig. 24). Posterior wall of R base (bearing anterior plate, usually on a prominence) and area anterior of 1A base (with posterior plate) are closely opposed to each other and presumably contact during wing supination. The plates are constantly present in Pachyneuridae, Cramptonomyiidae, Bibionidae (less sharply delimited in these three), Mycetophilidae s.l., Sciaridae, Cecidomyiidae, Synneuridae, Scatopsidae, and Anisopodidae s.l., but not found in Axymyiidae and Perissommatidae. In Brachycera this proprioceptive contact is provided with chordotonal organ inside R base (Zacwilichowski, 1931: Figs 28, 39, 43, 44) near the anterior process of 1A base, but devoid of hair plates; a pair of small sclerotized prominences retained in Tabanidae indicates that the condition is probably derivable from that of Bibionomorpha. A close contact of R and 1A bases is recorded also in some Tipuloidea and Ptychopteridae, but no special structures are developed in the case. In Culicoidea and Thaumaleidae a similar, but obviously non-homologous pair of sensory prominences is found in more proximal position: on R base near basiradiale and at 3rd axillary sclerite (i.e. within jugal lobe); they presumably contact at the end of downstroke, and seem bare except in Dixidae (Fig. 6; hairs less modified than in Bibionomorpha). In Chironomidae, only the hair plate at 3rd axillary is retained, activated by counterpart hair plate at posterior notal wing process of mesonotum when the wings are in resting position (proprioceptive contact of this type seems widespread, so far as incipient hair plate at notal process occurs e.g. in *Bibio*). Parallel reduction of radial hair plate in Culico- and Asilomorpha implies the chordotonal organ found in the latter was acquired already by Nematocera.

TAXONOMY

Key to the Triassic Diptera (based on wings)

1. Rs with 4 branches, R2 present at least as crossvein. Strong convex M base between R and Cu bases 2
— Rs with 2—3 branches, R2 lost. No distinct M base . . . . BIBIONOMORPHA 14
2. Wing area posterior to CuA narrow, hind margin nearly straight 3
— Area posterior to CuA broader, anal lobe produced. Sc terminating at or beyond wing midlength 5
3. Sc apex beyond wing midlength, *sc-r* before Sc midlength. R2 free. R2+3+4 stalk present, strong R5 convexity continued basad. M base stronger than R base. . . . . PSYCHODOMORPHA: **Hennigmatidae** Shcherbakov, fam. n.: M1+2 forking before *im* . . . . *Anemeca liya* Shcherbakov, gen. et sp. n.
— Sc apex much before wing midlength, *sc-r* terminal. No free R2. R4+5 stalk present, R5 weakly convex. R base stronger than M base. M1+2 forking beyond *im*. . . . . TIPULOMORPHA: ?**Limoniidae**: **Gnomuscinae** Shcherbakov, subfam. n.: . . . . *Gnomusca* Shcherbakov, gen. n. . . . 4
4. R4+5 forking distad of both CuA apex and *r-m*, the latter before midlength of *d* cell. Rs branches nearly straight . . . . *G. molecula* Shcherbakov, sp. n.
— R4+5 forking proximad of both CuA apex and *r-m*, the latter beyond midlength of *d* cell. Rs branches arcuate . . . . *G. renyxa* Shcherbakov, sp. n.

5\. Convex 1A reaching margin. R5 convexity restricted to the vein. CuP subparallel to CuA. Rs origin at 0.32—0.41, M forking at 0.48—0.54, and CuA apex at 0.64—0.78 of wing length . . . . other TIPULOMORPHA . . . 6

— 1A distally reduced, not reaching margin. R5 convexity continued along Rs up to MA. CuP strongly diverging from CuA. Rs origin at 0.14—0.27, M forking at 0.28—0.38, and CuA apex at 0.47—0.60 of wing length . . . . other PSYCHODOMORPHA 11

6\. Short R2 entering margin near R1. Rs forking at or before Sc apex level, CuA apex nearer to the latter than to R1 apex level . . . . **Vladipteridae** Shcherbakov, fam. n. . . 7

— Crossvein-like R2 entering R1 near margin. Rs forking beyond Sc apex level, CuA apex nearer to R1 apex level. *ia* and alular incision absent. . . . **Limoniidae**: **Architipulinae**. . . 10

7\. R5 originating distad of Sc apex. *m-cu* beyond midlength of *d* cell. 2A distant from margin and longer than half 1A. No alular incision. . .**Vladipterinae** Shcherbakov, subfam. n. . 8

— R5 originating proximad of Sc apex. *m-cu* before midlength of *d* cell. Submarginal 2A joined to 1A with oblique crossvein and not longer than 1/3 1A. Alular incision developed. . . . . . **Psychotipinae** Shcherbakov, subfam. n.: R4+5 very short or not developed. M1+2 forking beyond *im* . . . . *Psychotipa* Shcherbakov, gen. n. . . . 9

8\. R stem beyond sharp kink longer than Rs stem. M1+2 forking beyond *im* . . . . *Vladiptera kovalevi* Shcherbakov, gen. et sp. n.

— R stem beyond shallow kink shorter than Rs stem. M1+2 forking before *im* . . . . *Dilemmala specula* Shcherbakov, gen. et sp. n.

9(7). R4 forming short stalk with R5. R stem beyond kink longer than Rs. R2 shorter than half R3. *d* cell shorter than M branches beyond it . . . . . *Psychotipa predicta* Shcherbakov, sp. n.

— R4 forming short stalk with R2+3. R stem beyond kink shorter than Rs stem. R2 about half R3. *d* cell longer than M branches beyond it . . . . *P. depicta* Shcherbakov, sp. n.

10(6). R4 forming short stalk with R5. M forking basad of Rs fork and level to Sc apex. First *r-m* just distad of *m-cu*. M1+2 stalk beyond *im* much shorter than M1 . . . . *Mabelysia charlesi* Shcherbakov, gen. et sp. n.

— R4 forming short stalk with R2+3. M forking level to Rs fork, Sc apex just basad of both. *r-m* much basad of *m-cu*. M1+2 stalk beyond *im* longer than M1 . . . . *Architipula youngi* Krzeminski

11(5). Wing broad. Strongly convex R5 originating well before R4. M base stronger than R base. Rs origin close to MA. R2 free . . . . **Hennigmatidae** Shcherbakov, fam. n.: R2 longer than R2+3. Nodal line (with R2+3+4 bend) and pterostigma distinct . . . . . . **Kuperwoodiinae** Lukashevich, subfam. n.: . . . . *Kuperwoodia benefica* Lukashevich, gen. et sp. n.

— Wing rather narrow. R5 forming stalk with R4. R base stronger than M base. . . . . **Ptychopteroidea** . . . 12

12\. R2 crossvein-like, joining R1. R2+3 nearer to R1 than to R4, or equidistant from both. M1+2 aligned with M stem. M3+4 bent at *m-cu* (in proximal 1/3). CuP distally strong, convex and curved backwards from straight claval fold running to CuA apex . . . **Eoptychopteridae**: R2+3 equidistant from R1 and R4. R4+5 about 1/3 R5 . . . gen. et sp. indet. (Krzeminski, 1992c) (see Remarks under the family)

— R2 free, entering margin. R2+3 nearer to R4 than to R1. M forking rather symmetrically. M3+4 straight at *m-cu* (in distal 1/2). CuP weak and concave throughout . . . . **Nadipteridae** Lukashevich, fam. n.: . . . . *Nadiptera* Lukashevich, gen. n. . . . 13

13\. R2 longitudinal, R2+3 fork narrow. Rs origin much nearer to MA than to M fork. *d* cell shorter than M1+2 +M1 beyond it. CuA apex just distad of Sc apex . . . . *Nadiptera kaluginae* Lukashevich, sp. n.

— R2 oblique, R2+3 fork triangular. Rs origin halfway between MA and M fork. *d* cell longer than M1+2 +M1 beyond it. CuA apex proximad of Sc apex . . . . *N. pulchella* Lukashevich, sp. n.

14(1). Rs with 2 branches. *im* absent . . . . **Anisopodoidea?**: **Crosaphididae**: *Crosaphis anomala* Evans

— Rs with 3 branches. *d* cell closed with *im* 15

15\. Rs originating much proximad of M fork and forking before *r-m*. R4+5 forking much proximad of R1 apex, R4 nearly as long as R5 . . . 16

— Rs originating just proximad of M fork and forking just beyond *r-m*. R4+5 forking distad of R1 apex, R4 less than half R5 . . . . **Pachyneuroidea?**:**Alinkidae**: *Alinka cara* Krzeminski (on systematic position of the fossil see below)

16\. *m-cu* joining M3+4 . . . . **Pachyneuroidea**: **Procramptonomyiidae**: R4+5 forking before *r-m* . . . . *Yala argentata* Krzeminski

— *m-cu* joining M4 just beyond M3+4 fork. R4+5 forking beyond *r-m* . . . .
Anisopodoidea: **Protorhyphidae**: ***Vymrhyphus*** Blagoderov, gen. n. 17

17. R1 apex nearly level to M2 one, R5 diverging from R4 distally and entering beyond wing tip. CuA apex nearly halfway between M4 and CuP apices . . . .
. . ***Vymrhyphus tuomikoskii*** Blagoderov, sp. n.

— R1 apex proximad of M3 one. R5 subparallel to R4 except near apex, entering wing tip. CuA apex nearer to CuP than M4 apex . . .
. . . . ***V. triassicus*** Blagoderov, sp. n.

NEW MESOZOIC DIPTERA

Infraorder TIPULOMORPHA

VLADIPTEROIDEA Shcherbakov, superfam. n.

VLADIPTERIDAE Shcherbakov, fam. n.

Diagnosis. Wing: Short R2 joining margin near R1. R4+5 short (or R4 originating from R5 base), R5 convexity not continued basad. M fork rather symmetrical, at or just before wing midlength. M3+4 forking about *m-cu*. CuA distally curved backwards. CuP not strongly diverging from CuA. Convex 1A rather long, slightly bisinuate, weakening distally, reaching margin. 2A not shorter than 1/5 1A.

Two subfamilies included.

Comparison. Distinct from both Trichoceroidea and Tipuloidea in free R2 and better developed 2A.

VLADIPTERINAE Shcherbakov, subfam. n.

Diagnosis. Wing: *sc-r* presectoral. R5 originating distad of Sc apex. *m-cu* beyond midlength of *d* cell. 2A distant from margin, longer than half of 1A; *cu-a* and *ia* hardly traceable. Anal lobe but slightly produced; no alular incision.

Two following genera included.

Relationships. More primitive in claval structure than all the other Diptera, but already possessing all groundplan apomorphies of the order (see below). Included in Tipulomorpha, not Psychodomorpha, because the structure of claval area is least derived in the former.

Vladiptera Shcherbakov, gen. n.

Type species *Vladiptera kovalevi* Shcherbakov, sp. n.

Diagnosis. Wing: *sc-r* much before Rs origin. R kink sharp, R stem beyond it longer than Rs. R2 subtransverse. R4+5 forking nearly symmetrically at *r-m*. M stem with 'spur' continued basad between R and M bases but joining neither. M1+2 forking far beyond *im*. 1A about half of CuP.

Monobasic.

The genus and species are named in honour of our colleague dipterologist, the late Dr Vladimir G. Kovalev.

Vladiptera kovalevi Shcherbakov, sp. n.
(Figs 17, 24)

Holotype. Right wing PIN 2497/305 (part and counterpart), deformed (in 1st radial, medial, posterior cubital spaces); Kendyrlik syncline between Saur and Saikan Mts., East Kazakhstan; Triassic, upper Tologoi Formation.

Description. Wing 3.8 mm long, pale, veins and pterostigma dark. Venation as figured (initial wing shape restored at the figure).

Dilemmala Shcherbakov, gen. n.

Type species *Dilemmala specula* Shcherbakov, sp.n.

Diagnosis. Wing: *sc-r* just before Rs origin. R kink shallow, R stem beyond it shorter than Rs. R2 oblique. R4+5 forking symmetrically. M stem desclerotized except before fork. M1+2 forking before *im*.

Monobasic.

Remarks. The genus is provisionally assigned to the subfamily, because the structure of anal veins remains unknown.

Dilemmala specula Shcherbakov, sp. n.
(Fig. 18)

Holotype. Left wing 3288/288 (negative impression), incomplete (most of anal area and part of discal one missing) and deformed (along M1; fragment containing first Rs fork displaced); Madygen 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

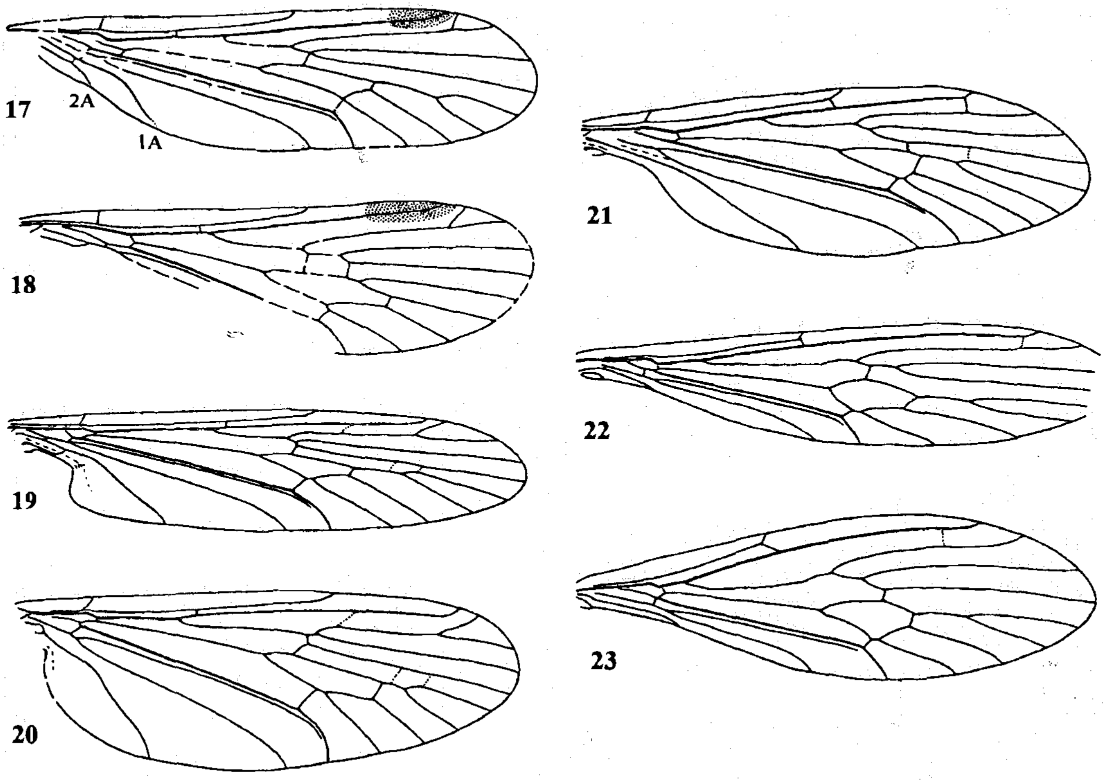
Description. Wing 3.8 mm long, pale, veins and pterostigma darker. Venation as figured (initial wing shape restored at the figure). Two *r-m* joining R4+5 and R5 bases.

PSYCHOTIPINAE Shcherbakov, subfam. n.

Diagnosis. Wing: *sc-r* postsectoral. R5 originating proximad of Sc apex. *m-cu* before midlength of *d* cell. 2A partly marginal, shorter than 1/3 1A and connected to it by oblique *ia*, forming anal loop. Anal lobe produced, alular incision distinct.

Monobasic.

Relationships. The group is transitional from Vladipterinae to Nadipteridae (Psychodomorpha) in retaining complete 1A when anal loop and alular



Figs 17—23. Venation (holotypes).

17—20: Triassic Vladipteridae, **17**, *Vladiptera kovalevi* sp. n.; **18**, *Dilemmala specula* sp. n.; **19**, *Psychotipa predicta* sp. n.; **20**, *P. depicta* sp. n. Reconstructed parts of veins in broken, folds in dashed line. Initial wing shape restored in **17** and **18**; **21—23:** Triassic Limoniidae,: **21**, *Mabelysia charlesi* sp. n.; **22**, *Gnomusca molecula* sp. n.; **23**, *G. renyxa* sp. n.

incision are already developed. Its allocation to Tipulomorpha seems to be a matter of convenience (so far as 1A is better recognisable in fossils), but it is further supported by the R5 convexity not continued basad, and wing proportions (see key above) more similar to Vladipterinae and Limoniidae. Supernumerary *r-rs* (see diagnosis of *Psychotipa*) occurs in *Dicranota* (Limoniidae Pediciinae), supernumerary *r-m* in *Protipula crassa* (Limoniidae Architipulinae; Handlirsch, 1906-1908) and *Neoderus patagonicus* (Tanyderidae; Alexander, 1927c).

Psychotipa Shcherbakov, gen. n.

Type species *Psychotipa predicta* Shcherbakov, sp. n.

Diagnosis. Wing: *sc-r* just before Rs origin. R kink small but distinct. R2 oblique. Rs nearly aligned with R4, *r-m* joining R5 base. M1+2 forking far beyond *im*. 1A a little longer than half of CuA. Supernumerary crossveins seem to be present, proximal *r-rs* and (two?) distal *r-m*.

Two following species included.

Psychotipa predicta Shcherbakov, sp. n.

(Figs 19, 36)

Holotype. Right wing PIN 2785/2490 (part and counterpart); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 5.5 mm long, pale, veins slightly darker. Venation as figured. Rs originating distally (shorter than R stem beyond kink), dividing into R2+3 and very short R4+5 stalk, R2 short and obligue. *d* cell rather short. *h* subtransverse. Free M base short, oblique.

Psychotipa depicta Shcherbakov, sp. n.

(Fig. 20)

Holotype. Left wing PIN 2555/661 (positive impression); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 5.6 mm long, uniformly pale. Venation as figured. Rs originating proximally (longer than R stem beyond kink), dividing into very short R2+3+4 stalk and R5, R2 longer and less oblique. *d* cell rather long. *h* oblique and slightly curved. Free M base longer, parallel to CuA.

Remarks. Despite the considerable differences of probably generic rank, we treat both species as congeners until the further specimens become known.

LIMONIIDAE (Rondani, 1856)
ARCHITIPULINAE Handlirsch, 1906

So far as known, this Mesozoic subfamily is indistinguishable from some Eriopterinae (e.g. *Cladura*) and (by wings) also from some Hexatominae (e.g. *Limnophila, Pilaria, Ulomorpha*), differing from the latter in the loss of tibial spurs (Kalugina & Kovalev, 1985). It should be noted that two latter genera are the only Tipuloidea with larval mandibles bifold (supposed ground-plan condition; see below), but usually considered as highly specialized forms (Oosterbroek & Theowald, 1991).

The wings of Trichoceridae (known since the Early Jurassic) differ from those of primitive Limoniidae only in the length of 1A, the character seeming rather tenuous if we compare trichocerid *Diazosma* (1A about half of CuP) with some Eriopterinae (about half of CuA; Alexander, 1967: Figs 394, 452). Such moderately long 1A, characteristic also of Vladipteridae, is more primitive than both shorter one of typical Trichoceridae and longer one of most Tipuloidea. The crucial body characters are untraceable in most Mesozoic fossils assigned to Limoniidae, and some of these extinct taxa (especially Triassic ones) could be primitive enough to retain ocelli, free cardo and amphipneustic larva with nonretractile head, representing in fact primitive Trichoceroidea with 1A not shortened yet.

Mabelysia Shcherbakov, gen. n.

Type species *Mabelysia charlesi* Shcherbakov, sp.n.

Diagnosis. Wing: Sc joining C at wing midlength, *sc-r* terminal. R kink shallow. Rs dividing into R2+3 and very short R4+5 stalk, R2 joining R1 near margin. M forking symmetrically at Sc apex level, basad of Rs fork. *d* cell triangular, (first) *r-m* joining it just before *im* and distad of *m-cu* (the latter just before M3+4 fork), M1+2 stalk beyond *im* short (about 1/4 of M1). CuA apex nearly level with R1 apex. 1A slightly bisinuate, ca. 0.6X CuA. Free 2A very short. Anal lobe somewhat produced.

Monobasic.

Comparison. More primitive in wing characters than other genera. So far as known, unique in the *r-m* joining triangular *d* cell near its apex. Also distinct from most extinct and recent taxa in the Rs forking into R2+3 and R4+5 distad of both Sc apex and M fork (like in *Ulomorpha quinquecellula*; Alexander, 1967), and M forking at wing midlength (like in some *Molophilus* spp.).

The genus and species are named in honour of eminent dipterologist, the late Dr Charles P. Alexander, and his wife Mabel.

Mabelysia charlesi Shcherbakov, sp. n.
(Figs 21, 25)

Holotype. Left wing PIN 2069/3541 (part and counterpart); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 5.2 mm long, pale, veins slightly darker. Venation as figured. Supernumerary *r-m* seems present.

?LIMONIIDAE
GNOMUSCINAE Shcherbakov, subfam. n.

Diagnosis. Wing: Sc apex much before wing midlength, *sc-r* terminal. R stem beyond distinct kink short. R kink sharp. No free R2 (submarginal crossvein-like one seems present). M1+2 forking beyond *im*, *m-cu* joining M3+4 just before fork. 1A short (much less than half of CuA), 2A very short but distant from margin. Area posterior to CuA narrow, hind margin straight; neither anal lobe nor alular incision developed.

Monobasic.

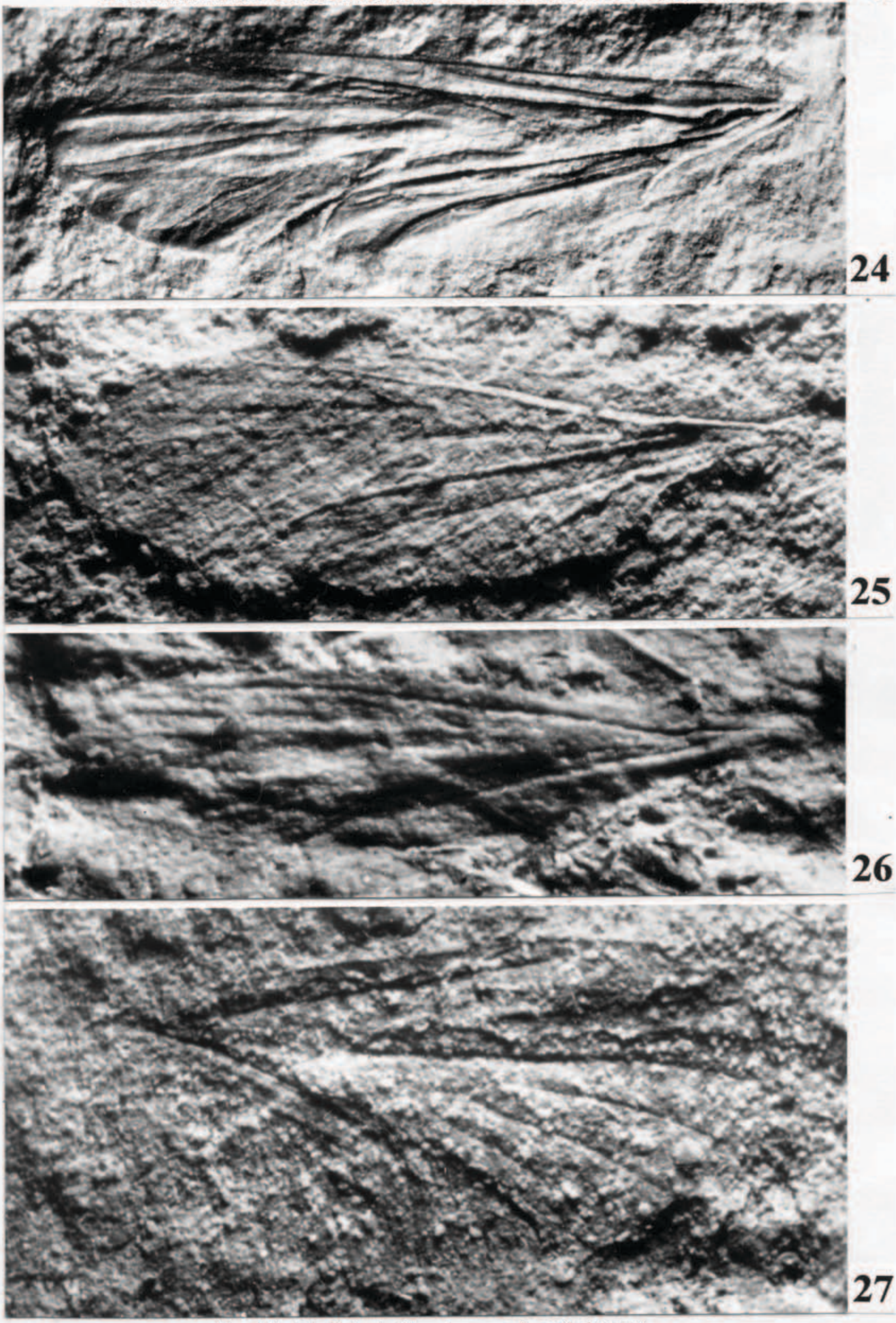
Relationships. Resembling Psychodidae in the short Sc, proximal Rs origin and undeveloped anal lobe, but otherwise, especially in basiala structure, consistent with Tipulomorpha. Similar to Trichoceridae in the shortening of 1A, but distinct (and similar to Tipuloidea) in *sc-r* terminal and probably also R2 submarginal. Provisionally assigned to Limoniidae, but could be rather an independent offshoot from Vladipteridae, homoplastic with Tipuloidea in the two latter characters. Distinct from other Tipulomorpha in the short Sc and 1A, combined with pentagonal *d* cell and main forks not distalized.

Gnomusca Shcherbakov, gen. n.

Type species *Gnomusca molecula* Shcherbakov, sp.n.

Diagnosis. Wing: Rs originating early (somewhat distad of R kink), slightly bent proximad of M fork, forking about wing midlength; R4+5 rather short; R2 seems to join R1 near margin. M forking symmetrically basad of Rs fork. *d* cell pentagonal, *r-m* joining it just distad of *m-cu*, M1+2 stalk beyond *im* long (about half of M1).

Two following species included.



Figs 24—27. Triassic Nematocera, wings (holotypes).
24, *Vladiptera kovalevi* sp. n.; *25*, *Mabelysia charlesi* sp n.; **26,** *Gnomusca molecula* **sp.** n.; **27,** *Kuperwoodia benefica* **sp.** n.

Gnomusca molecula Shcherbakov, sp. n.
(Figs 22, 26)

Holotype. Right wing PIN 2785/4096 (negative impression); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 3.0 mm long, pale, veins slightly darker. Venation as figured. R4+5 forking distad of both CuA apex and *r-m*, the latter before midlength of *d* cell. Rs branches nearly straight.

Gnomusca renyxa Shcherbakov, sp. n.
(Fig. 23)

Holotype. Left wing PIN 2069/3756 (part and counterpart); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 3.4 mm long, pale, veins slightly darker. Venation as figured. R4+5 forking proximad of both CuA apex and *r-m*, the latter beyond midlength of *d* cell. Rs branches arcuate.

Infraorder PSYCHODOMORPHA
Superfamily PTYCHOPTEROIDEA
NADIPTERIDAE Lukashevich, fam. n.

Diagnosis. Wing: Sc apex beyond wing midlength, *sc-r* much proximad of it, beyond Rs origin. Free R2 joining wing margin, R2+3 fork if rather long then narrow, R4+5 at least 3.7 times shorter than R4+5 fork, R5 convexity continued along Rs up to MA. M forking rather symmetrically, *d* cell long, *m-cu* joining M3+4 (beyond its midlength) with straight CuA. Long convex free M base aligned with CuA. CuP weak, concave and strongly diverging from CuA for its entire length. 1A beyond oblique *cu-a* converging to and reaching near CuP. 2A forming narrow anal loop.

Monobasic.

Age. Triassic — Jurassic.

Relationships. The group is symplesiomorphous with Tanyderidae in retaining free R2, but placed in Ptychopteroidea on account of *sc-r* proximal, R4 not aligned with Rs, M1+2 forking beyond *im* (see generic diagnosis; all symplesiomorphies with other ptychopteroids and Vladipteridae), narrow anal loop with 1A traceable beyond *cu-a* (symplesiomorphy), M3+4 forking beyond *m-cu*, and CuP strongly diverging from CuA (synapomorphies). Tanyderidae (still not recorded in the Triassic) are apomorphic in the above characters (except two latter), and the rather long free R2 in most tanyderids and some psychodids turns out secondary, if compared to quite short one in all known Liassic members of these two families (Ansorge, 1994) and even shorter oblique one almost touching R1 apex in very primitive *Vladiptera*.

Nadiptera Lukashevich, gen. n.

Type species *Nadiptera kaluginae* Lukashevich, sp.n.

Diagnosis. Wing: R kink small or indistinct. Rs origin much proximad of M fork, Rs stem long and straight, nearly aligned with straight R4+5. *r-m* beyond Rs fork and nearly level with M3+4 fork. M1+2 forking beyond im.

Three following species included.

The genus and type species are named in honour of our colleague dipterologist, the late Dr Nadezhda S. Kalugina.

Nadiptera kaluginae Lukashevich, sp. n.
(Fig. 28)

Holotype. Left wing PIN 1361/1 (negative impression); Kysyltam, northern slope of Ketmen' Mts., South Kazakhstan; Triassic, Koldzat Formation.

Description. Wing 4.7 mm long, pale, veins slightly darker. Venation as figured. Rs originating early, somewhat distad of MA. R2 longitudinal, slightly shorter than R2+3 stem, entering margin halfway between R1 and R3; R2+3 fork very narrow. R2+3 much nearer to R4 than to R1. R5 aligned with R4+5. *r-m* at midlength of R4+5 stalk and beyond midlength of *d* cell. *m-cu* before midlength of *d* cell. Proximal CuA section (up to *m-cu*) 1.8X distal one, the latter slightly arcuate, entering margin just distad of Sc apex. CuP slightly arcuate. Free 2A apex traceable.

Nadiptera pulchella Lukashevich, sp. n.
(Figs 29, 37)

Holotype. Right wing PIN 2555/660 (positive impression); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 4.2 mm long, slightly infuscated, veins pale. Venation as figured. Rs originating later, about halfway between MA and M fork. R2 oblique, short, entering margin near R1; R2+3 fork triangular. R2+3 much nearer to R4 than to R1. R5 aligned with R4+5. *r-m* just beyond Rs fork and before midlength of *d* cell. *m-cu* before midlength of *d* cell. Proximal CuA section 1.9X distal one, the latter curved backwards, entering margin proximad of Sc apex. CuP nearly straight.

Nadiptera anachrona Lukashevich, sp. n.
(Fig. 30)

Holotype. PIN 371/926 (negative impression), poorly preserved male (?) lacking head; Sogyuty near Issyk-Kul' Lake, Kyrgyzstan; Lowermost Jurassic, Dzhil Formation.

Description. Wings 5.5 mm long, pale. Venation as figured. Rs originating early, twice nearer to MA than to M fork. R2 longitudinal, twice shorter than R2+3 stem, entering margin nearer to R1; R2+3 fork narrow. R2+3 a little nearer to R4 than to R1. R4+5 forking symmetrically. *r-m* at R5 base and near apex of *d* cell. *m-cu* beyond midlength of *d* cell. Proximal CuA section 4X distal one, the latter curved backwards, entering margin at the same level as Sc. CuP distinctly arcuate. Body slender, legs long, genitalia broader than preceding segments.

Comparison. Similar to *N. kaluginae*, but distinguishable by the symmetrical R4+5 fork, longer *d* cell and more distal position of *r-m* and *m-cu*.

Remarks. More similar to Eoptychopteridae than other two species, in the R2+3 nearly equidistant from R1 and R4, and CuP distinctly arcuate. Despite the considerable differences of probably generic rank, we provisionally treat all three species as congeners.

HENNIGMATOIDEA
Shcherbakov, superfam. n.

HENNIGMATIDAE Shcherbakov, fam. n.

Diagnosis. Wing with main forks and crossveins more or less shifted to base. Sc apex beyond wing midlength. R base up to MA weak. Rs originating very early, close to MA. R2+3+4 aligned with Rs stem, forking symmetrically into R2+3 and R4. Strongly convex R5 (its convexity continuing basally up to MA) separating before wing midlength, much earlier than R4. Strong convex M base aligned with CuA. M branches beyond *d* cell long. CuP diverging from CuA. Often alular incision distinct and anal lobe prominent.

Two subfamilies included.

Relationships. The unique combinations of characters is unknown in other Diptera. Early separation of both Rs and R5 combined with free R2 is characteristic of some psychodids (Phlebotominae), but Sc is very short and *sc-r* terminal in the case. Long R(2+)3+4 stalk occurs also in some Blephariceridae (*Edwardsina nigra*; Edwards, 1929), and R5 convexity is traceable basad in some members of the family, but the other characters are dissimilar. Early separation of Rs and basal continuation of R5 convexity (as well as nodal flexion) are usual in Asilomorpha, but overall venation has nothing in common. Broad wing with large anal lobe, conspicuous nodal flexion line and pterostigma is known also in Eoptychopterininae, but Rs pattern is different in the latter. In *Kuperwoodia* the anal loop is shaped like in Tanyderidae and primitive Psychodidae (*Nemapalpus*), both retaining some nodal flexion, but CuP turns convex distally like in Eoptychopteridae and Ptychopteridae. The new family resembles Psychodoidea and Blephariceridae in the Rs aligned with R2+3+4, but in both Rs origin and M fork very proximal, R5 convexity continued up to MA, and CuP diverging from CuA, it is similar to and possibly derivable from Nadipteridae (or rather from their precursors with *m-cu* still about M3+4 fork). The group is unique in basiala structure (with R stem weak) and deserves superfamily of its own.

KUPERWOODIINAE Lukashevich, subfam. n.

DIAGNOSIS. Wing: Nodal flexion line and pterostigma well developed. R2 longer than R2+3; 1st radial space broadened. M stem (beyond MA) as long as *d* cell, both rather short. CuA bent at *m-cu* and then strongly diverging from M4; *m-cu* before wing midlength. Anal loop broad, 1A joining Cu base.

Monobasic.

Kuperwoodia Lukashevich, gen. n.

Type species *Kuperwoodia benefica* Lukashevich, sp. n.

Diagnosis. Wing broad with anal lobe produced. Sc close to R1. R2+3+4 angulately bent forwards at nodal level. Long R2 running across broad 1st radial space along outer margin of pterostigma. *im* before M1+2 fork, *m-cu* just beyond M3+4 fork. M branches much stronger distally than at *d* cell. Proximal CuA section (up to *m-cu*) ca. 1.5X distal one. CuP turning convex distally.

Monobasic.

The genus is named in honour of Kuperwood Enterprises Co. for financial support of paleoentomological studies.

Kuperwoodia benefica Lukashevich, sp. n.
(Figs 27, 31)

Holotype. Left wing PIN 2344/490 (negative impression); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 3.3 mm long, infuscated, veins and pterostigma darker. Venation as figured. Supernumerary *r5-m1* seems present.

HENNIGMATINAE Shcherbakov, subfam. n.

DIAGNOSIS. Wing: Nodal flexion line and pterostigma untraceable. R2 shorter than R2+3; 1st radial space of usual width. M stem much shorter than long *d* cell. CuA straight at *m-cu* and curved backwards before apex; *m-cu* beyond wing midlength. Anal loop narrow.

Two genera included.

Age. Triassic — Cretaceous.

Anemeca Shcherbakov, gen. n.

Type species *Anemeca liya* Shcherbakov, sp. n.

Diagnosis. Wing elongate with anal lobe reduced. Sc halfway between C and R1. Postsectoral *sc-r* nearly level with *d* cell base. M stem shorter than 1/3 of long *d* cell. M1+2 forking before *im* and M3+4 fork; *m-cu* beyond M3+4 fork. M branches much stronger distally than at *d* cell. Proximal CuA section thrice as long as distal one. CuP weak distally. Anal loop very short, 1A beyond it rather long; no alular incision.

Monobasic.

Anemeca liya Shcherbakov, sp. n.

(Fig. 32)

Holotype. Left wing PIN 2069/3354 (negative impression); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 6.0 mm long, pale, veins dark. Venation as figured. Supernumerary subbasal *r-m* seems present.

Hennigma Shcherbakov, gen. n.

Type species *Hennigma cladistorum* Shcherbakov, sp. n.

Diagnosis. Wing rather broad with anal lobe produced. Sc close to R1 except distally, with few transverse veinlets not reaching C. Two postsectoral *sc-r*, first just beyond *h*, second nearly level with R5 origin. M stem extremely short, so the base of unusually long *d* cell close to MA. *im* well before M1+2 fork, *m-cu* just before M3+4 fork. M branches weak. Weak concave fold developed anterior to CuA, reaching level of R5 origin. Proximal CuA section more than twice as long as distal one. CuP weak distally. Anal loop narrow, longer than 1A beyond it, the latter aligned with 2A and terminating at deep alular incision. Supernumerary *r-rs* just beyond R4 origin.

Monobasic.

Age. Earliest Cretaceous.

Comparison. Distinct from Triassic *Anemeca* gen. n. in the broader wing with anal lobe, longer *d* cell, etc.

Remarks. Numerous subcostal veinlets are recorded also in *Gonomyia polingi* (Limoniidae, Eriopterinae; Alexander, 1967).

The genus is named in honour of eminent dipterologist, the late Dr Willi Hennig.

Hennigma cladistorum Shcherbakov, sp. n.

(Figs 33, 39)

Holotype. Right wing PIN 3965/2789(3290) (part and counterpart); Khutel-Khara 75 km SE Sain-Shand, East Gobi aimak, Mongolia; Lowermost Cretaceous (Uppermost Jurassic not excluded), lower Tsàgantsab Formation.

Description. Wing 8.9 mm long, pale, veins dark. Venation as figured. Weak supernumerary *r4-r5* and *r5-m1* present.

Infraorder BIBIONOMORPHA

Superfamily ANISOPODOIDEA

Family PROTORHYPHIDAE Handlirsch, 1906

Vymrhyphus Blagoderov, gen. n.

Type species *Vymrhyphus tuomikoskii* Blagoderov, sp. n.

Diagnosis. Wing elongate. Sc apex at or just beyond wing midlength, distad of *r-m*. R4+5 forking level to or just distad of *d* cell apex. R1, R2+3 and R4 nearly straight and subparallel for most of their lengths, all three and R5 equidistant at pterostigma level, their apices almost evenly spaced along margin. R5 but slighhtly arched forwards. *r-m* at or before *d* cell midlength. M3+4 forking before 1/4 *d* cell length. M4 base (before *m-cu*) shorter than 1/5 *m-cu*. Proximal CuA section (up to *m-cu*) at least 1.9X distal one, the latter subparallel to CuP.

Two following species included.

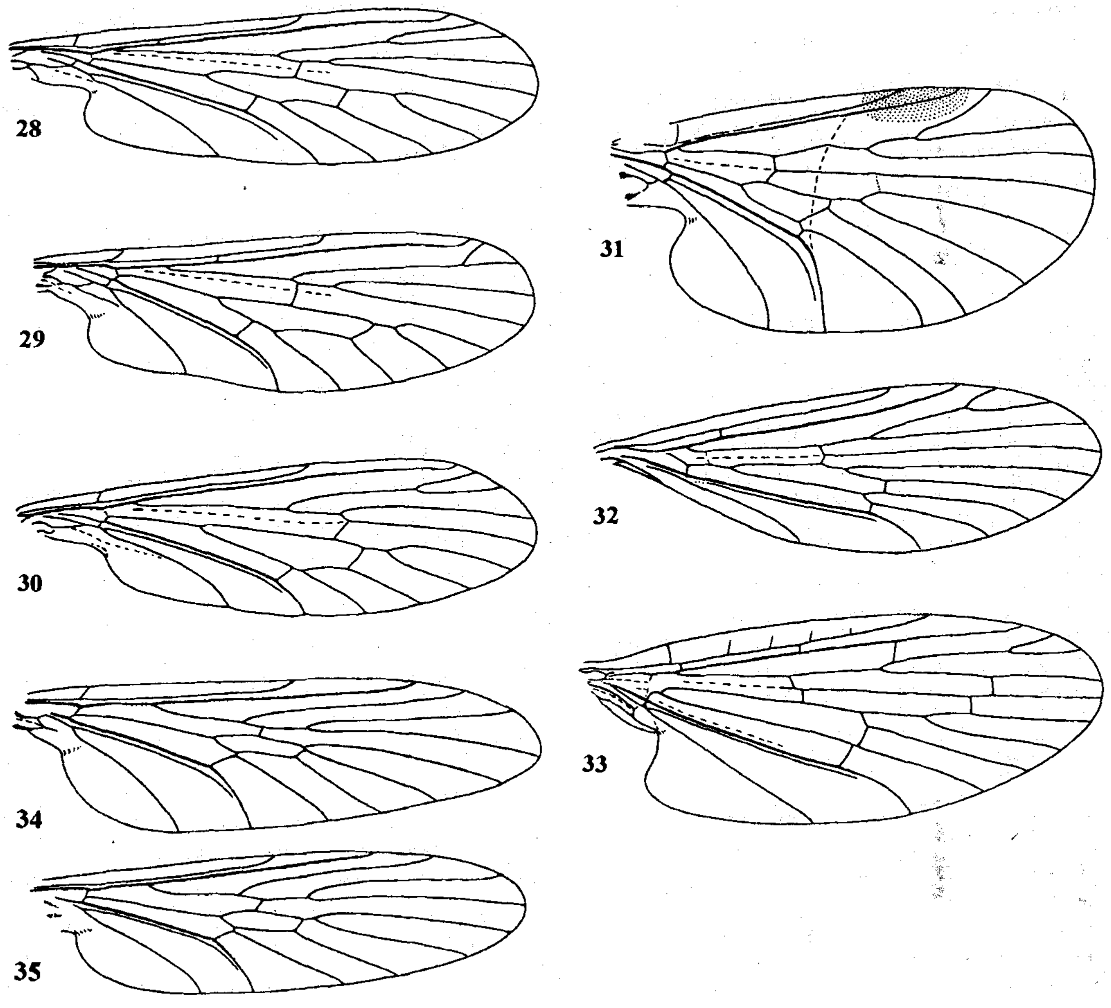
Comparison. In *Protorhyphus* Handlirsch and *Archirhyphus* Handlirsch the wing broader, Sc reaching at most 0.4 wing length (M fork level), R2+3 converging to R1 (and diverging from R4) apically, *r-m* beyond *d* cell midlength, and both M4 base and distal CuA section longer. (*Acritorhyphus* Bode is synonymized under *Eoptychoptera* Handlirsch — Ansorge, Lukashevich & Krzeminski, in prep.; *Heterorhyphus* Bode does not belong to the family — Ansorge & Krzeminski, in press, b).

Vymrhyphus tuomikoskii Blagoderov, sp. n.

(Fig. 34)

Holotype. Right wing PIN 2785/3052 (negative impression); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 2.2 mm long, pale, veins slightly darker. R1 apex nearly level to M2 one. R5 diverging from R4 distally and entering beyond wing tip. 1st basal cell narrower than 2nd one. M1+2 forking at *im*. CuA apex nearly halfway between M4 and CuP apices.



Figs 28—35. Wing venation (holotypes).

28—30, Mesozoic Nadipteridae: **28**, *Nadiptera kaluginae* sp. n. (Triassic), **29**, *N. pulchella* sp. n. (Triassic), **30**, *N. anachrona* sp. n. (Jurassic); **31—33**, Mesozoic Hennigmatidae: **31**, *Kuperwoodia benefica* sp. n. (Triassic), **32**, *Anemeca liya* sp. n. (Triassic), **33**, *Hennigma cladistorum* sp. n. (Cretaceous); **34—35**, Triassic Protorhyphidae: **34**, *Vymrhyphus tuomikoskii* sp. n., **35**, *V. triassicus* sp. n.

The species is named in honour of dipterologist Dr R. Tuomikoski.

Vymrhyphus triassicus Blagoderov, sp. n.

(Figs 35, 38)

Holotype. Right wing PIN 2069/3757 (negative impression); Dzhailoucho 30 km W Isfara, southern Fergana, Kyrgyzstan; Triassic, Madygen Formation.

Description. Wing 3.1 mm long, pale, veins slightly darker. R1 apex proximad of M3 one. R5 subparallel to R4 except near apex, entering wing tip. 1st basal cell not narrower than 2nd one. M1+2 forking just beyond *im*. CuA apex nearer to CuP than M4 apex.

On relationships of some Mesozoic families

ANSORGIIDAE

Krzeminski et Lukashevich, 1993

The family was described on two males from the Upper Jurassic of Kazakhstan (Krzeminski & Lukashevich, 1993; erroneously cited as Cretaceous in the title) as intermediate between Tanyderidae and Eoptychopteridae. There are several characters not indicated in the original description, which we believe now to be diagnostic at the family and generic level (Figs 40—43).

Diagnosis. Wings preserved with costal margins at about 60° (unusual for fossil Nematocera, thus implying specific wing position at rest). C continued beyond wing apex as ambient vein, bearing fringe of short hairs; Sc weak; *sc-r* about Rs fork level; free R2 absent (weak crossvein-like one might be present proximad of R4+5 fork); free M base strongly convex; both M1 and M2 weakly convex. Alular incision deep, anal lobe subrectangular. Antennae quite short, without conspicuous pubescence. Eyes very large, of large and sharply delimited facets. Ocellar tubercle seems present. Palpi as long as rather short rostrum, originating near its base. Mesonotum with V-shaped suture; middle coxae inserted close to hind ones. Legs relatively short, strong, prehensile (in holotype preserved with tibiae adduced to femora, like in the undescribed Late Cretaceous blepha-ricerids, and tarsi curved), with long powerful claws (no empodium visible); 1st tarsomere longest (about half of tarsus), 4th probably shortest; fore trochanters not elongated; fore femora, tibiae and tarsi longest, middle ones shortest. Male abdomen with seven pregenital segments visible, 7th rather short, 1th very short, 8th evidently very reduced. Gonocoxites fused to 9th sternite into rather small (narrower than 7th segment) capsule. Gonostyli double, with shorter inner gonostylus originating near base of heavily setose outer gonostylus. 10th tergite apically bilobed. 9th sternite preserved in nearly ventral position (visible at positive impression) whereas 10th tergite and inner gonostyli in dorsal position (at negative impression), i.e. genitalia not inverted and (taking into account their small size and reduction of 8th segment) might be dorsoflexed at life (like in blephariceridis and deuterophlebiids).

Ansorgius Krzeminski in Evenhuis, 1994

Ansorgia Krzeminski et Lukashevich, 1993, nom. praeocc.

(Only males known.) Flagellum tapering distally, with basal segments subquadrate, distal ones about twice as long as wide. Eyes dorsally separated by less than eye width. Fore legs slender, ca. 1.5 times as long as middle ones. Tibial spurs absent. Distal portion of hind tibia slightly curved, darkened, and bearing a series of stiff black setae at outer margin. 5th tarsomere slightly emarginate ventrally, with **pollex** (ventrobasal swelling with a cushion of black spiny setae) especially strong in hind legs. Claws ventrally setose, about 2/3 as long as 5th tarsomere. Outer gonostyli somewhat bilobed, apices of their longer dorsal lobes overlapping, inner margins of more incurved ventral lobes dentate. Inner gonostyli seem complex, with broad basal lobe (its outer margins sclerotized) and narrow sclerotized apical process.

Relationships. Instead of ptychopteroid affinities originally claimed, we prefer to associate the fossils in question with Blephariceroidea for the following reasons:

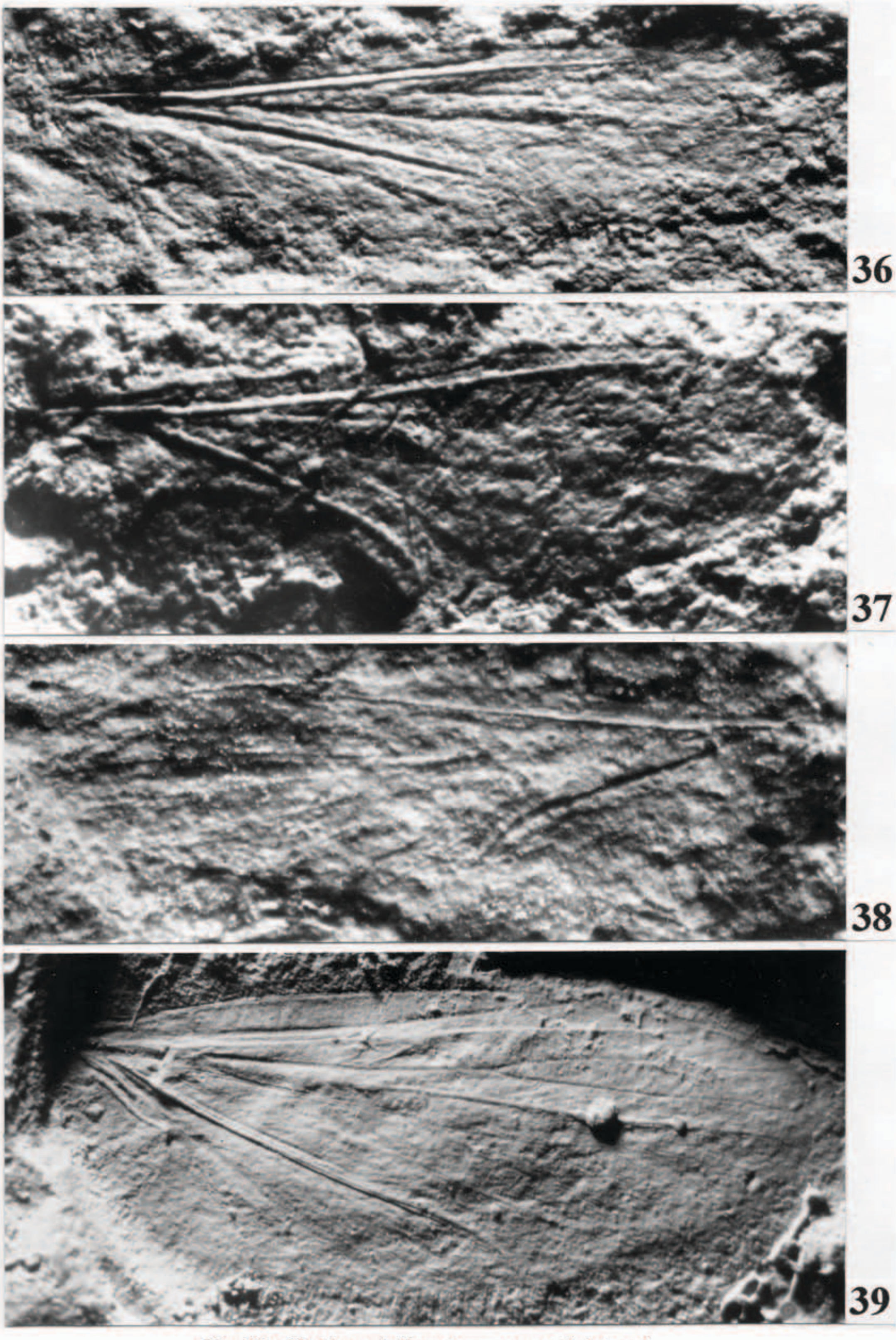
Ansorgiidae bear no special resemblance to Ptychopteroidea. R2 is always retained in the latter, at least as strong distal crossvein. M3+4 forking beyond *m-cu* is not unique to ptychopteroids, being characteristic (as well as the loss of R2) of Blephariceridae and some Psychodidae. Male genitalia of *Ansorgius*, originally described as resembling that of *Proptychopterina* Kalugina, in fact are surprisingly blephariceridlike.

Ansorgiidae are synapomorphic with Psychodoidea and Blephariceridae in the R4 aligned with short R4+5 and Rs stem (*r-m* joining R5 base). The presumed retention of ocelli in *Ansorgius* is symplesiomorphic with Blephariceridae (the loss of ocelli is still not confirmed in Mesozoic tanyderids).

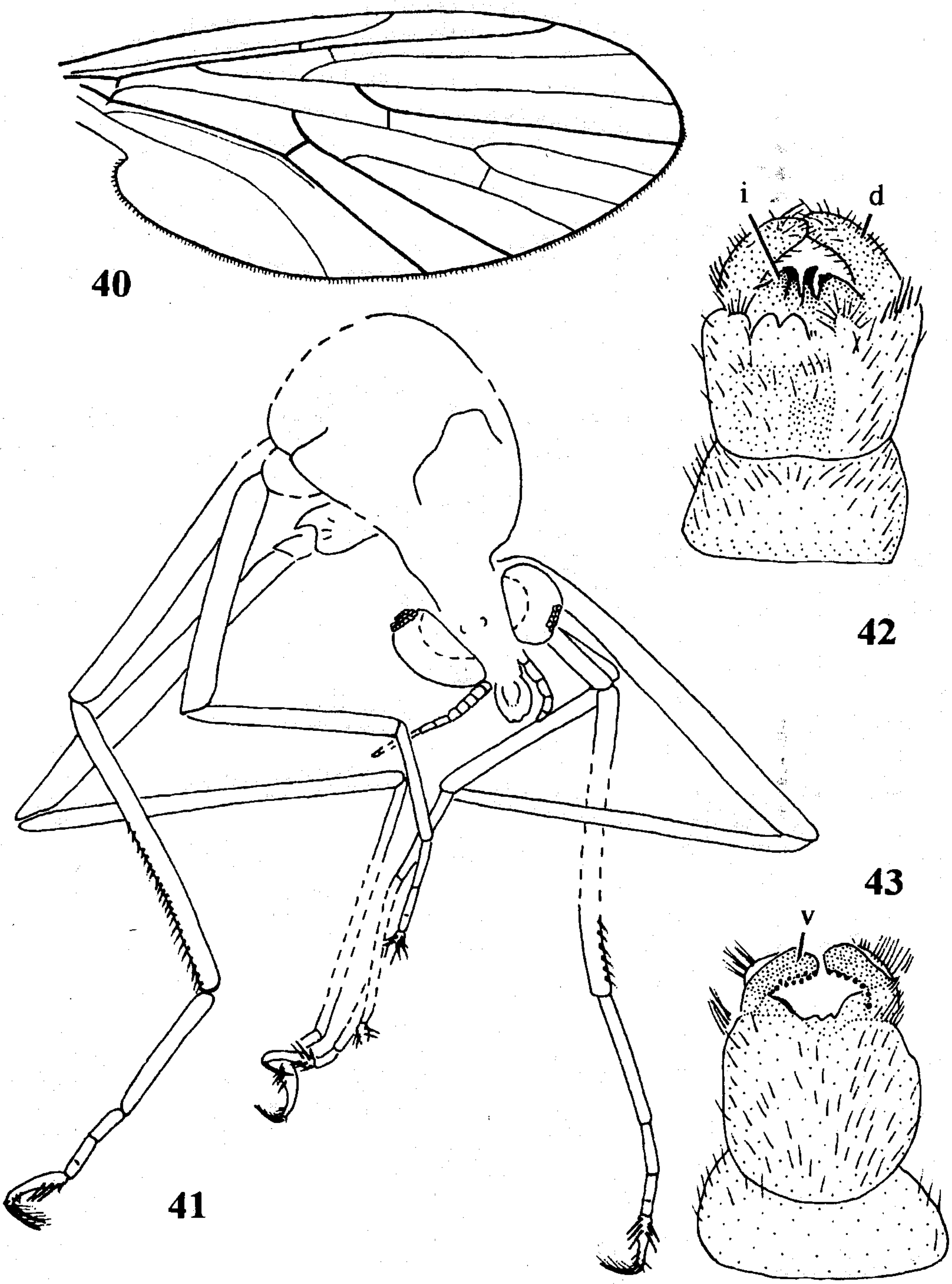
Numerous characters of Ansorgiidae could be interpreted as synapomorphies (or synapomorphic trends) with Blephariceridae: Sc weak or distally reduced; R2 shifted proximad or lost; antennae short; eyes large with large facets; legs prehensile; distitarsus with pollex; claws strong and ventrally setose; empodium reduced; male gonocoxites and 9th sternum fused into small capsule; gonostyli double; male legs tend to be curved and provided with peculiar setation; wings probably held flat and at a moderate angle from the body when at rest; male genitalia possibly dorsoflexed. Despite some of the above characters seeming rather tenuous, the whole bulk of evidence (and especially leg and genitalia structure) supports the blephariceridaffinities of Ansorgiidae quite well; therefore, we regard the latter as the most primitive (and still tanyderid-like) Blephariceroidea.

Long fore legs of *Ansorgius* are peculiar, with all the segments elongated (not only tarsi as e.g. in chironomids). They seem too slender to be grasping like the longest and stoutest hind legs in both sexes of Blepharicerinae s.l., used by the mandibulate female to hold onto its prey (Hogue, 1981). In Edwardsininae the differences in leg length are less marked, and fore tarsi are the longest (Zwick, 1977). Probably ansorgiids clung to perches with elevated fore legs when at rest, like the modern net-winged midges.

As judged from the complete venation with C continued around the wing, the network of secondary folds (enabling instant wing spreading in the emerging adult) was rather not developed yet in the Jurassic family. However, its members could,



Figs 36—39. Mesozoic Nematocera, wings (holotypes).
36, *Psychotipa predicta* sp. n. (Triassic); **37,** *Nadiptera pulchella* sp. n. (Triassic); **38,** *Vymrhyphus triassicus* sp. n. (Triassic); **39,** *Hennigma cladistorum* sp. n. (Cretaceous).



Figs 40—43. *Ansorgius predictus* (Krzeminski et Lukashevich) (Upper Jurassic).
40, venation (holotype PIN 2784/114); **41—43**, paratype PIN 2784/410(428): **41**, head, thorax and legs; **42—43**, male genitalia: **42**, dorsal view (from negative impression), **43**, ventral view (from positive impression); **d** — dorsal lobe of outer gonostylus, **v** — ventral lobe of outer gonostylus, **i** — inner gonostylus.

like blephariceridids, have been already confined to streams, both groups being extremely rare in the fossil record.

EOPTYCHOPTERIDAE Handlirsch, 1906

The Ptychopteroidea, now including one mostly Triassic, one mostly Jurassic and one extant family (known since the Cretaceous), seems to play an important role in the primary radiation of Oligoneura. Nadipteridae are presumably related to Tanyderidae and ancestral to Eoptychopteridae. The latter, recently revised by one of us (Lukashevich, 1993), turned out quite diverse in both wing and body structure, enough to be divided into three subfamilies (their separation at suprageneric level was first assumed by Kalugina in Kalugina & Kovalev, 1985).

Diagnosis. Wing: R2 crossvein-like, joining R1. R2+3 nearer to R1 than to R4, or equidistant from both. M stem more or less desclerotized, M1+2 aligned with it; *im* present; M3+4 bent in proximal third at *m-cu*. CuP turning convex and more sclerotized distally when curved backwards from straight claval fold running to CuA apex.

Remarks. The incompletely preserved Triassic specimen (its unpublished photographs were studied through the kindness of Dr W. Krzeminski) assigned to the family (Krzeminski, 1992c) demonstrates only one character matching with Eoptychopteridae rather than Nadipteridae (R2+3 equidistant from R1 and R4), far from being unique among the Nematocera. Neither R1 apex nor R2 could be located with certainty in the fossil, but the R3 is bent near apex, implying R2 position more distal than in other eoptychopterids. If the specimen really belongs to the latter family, it could be separated into a second genus of Proptychopterininae subfam. n., distinct from the Jurassic one in the Rs originating more distally and forking just before *r-m*, and R4+5 shorter. Otherwise it may represent one more genus of Nadipteridae.

Key to subfamilies of Eoptychopteridae

1. Antennae short, body rather stout. Rs angulate towards M stem; R4+5 bent at *r-m*. M3+4 simple. . . . . **Eoptychopterininae**

— Antennae long, body rather slender. Rs and R4+5 straight or slightly curved 2

2. Rs forking symmetrically, well before *r-m*. R2+3 nearly equidistant from R1 and R4. CuA nearly straight at *m-cu* and beyond it . . . . **Proptychopterininae**

— Rs continued rather with R4+5, forking just before or beyond *r-m*. R2+3 close to R1. CuA distinctly bent at *m-cu*, sometimes sigmoidal beyond it . . . . **Eoptychopterinae**

PROPTYCHOPTERININAE Lukashevich, subfam. n.

Diagnosis. Slender insects with elongate abdomen. Antennae long, flagellomeres cylindrical with few long setae. Wing narrow. *sc-r* just before or beyond very proximal Rs origin. Rs nearly straight, forking symmetrically; R2+3 nearly equidistant from R1 and R4. *r-m* about midlength of R4+5, joining M1+2 before *im*. M stem distinct. *im* well before M1+2 fork, M3+4 forked. CuA nearly straight at *m-cu* and beyond it. CuP arcuate near base, *cu-a* joining Cu about fork, 1A distad of *cu-a* usually retained as rather long spur (Fig. 15). Alular incision slight to absent, alula not developed.

The only genus included: *Proptychopterina* Kalugina, 1985.

Age. Early to Late Jurassic.

Relationships. The subfamily seems to be ancestral to remaining two. Being the most similar to Nadipteridae, it differs from it in the characters mentioned in the key to Triassic Diptera, and also in the longer R4+5 (at most 2.6 times shorter than R4+5 fork).

EOPTYCHOPTERINAE stat. n.

Diagnosis. Rather slender insects (*Crenoptychoptera*), or body more compact and (as well as wings) densely pilose, and flagellomeres of elongate antennae with few small setae (*Eoptychoptera*). Wing narrow. *sc-r* close to *h*. Rs straight or slightly curved, aligned with straight R4+5; R2+3 close to R1. *r-m* just before or beyond Rs fork, joining M1+2 near base. M stem distinct. *im* before (*Architendipes*) or beyond M1+2 fork, sometimes (*Crenoptychoptera*) M3+4 simple. CuP near base angulate at *cu-a*, 1A distad of the latter lost (at most short stub retained; see Fig. 5). Alular incision distinct to absent, rarely alula slightly produced.

Besides the type genus, *Eoptychoptera* Handlirsch, 1906 (= *Proptychoptera* Handlirsch, 1906 = *Palaeolimnobia* Bode, 1953 = *Acritorhyphus* Bode, 1953; Ansorge, Lukashevich & Krzeminski, in prep.), also *Architendipes* Rohdendorf, 1962 (Ansorge, Lukashevich & Krzeminski, in prep.) and *Crenoptychoptera* Kalugina, 1985.

Age. Early Jurassic to Early Cretaceous.

Relationships. The group is very similar to Ptychopteridae in both adult and pupal characters and clearly ancestral to it (therefore both families should be united under Ptychopteroidea) (Lukashevich, in press, a), so that the wing of *Crenoptychoptera* could be distinguished from that of recent *Ptychoptera* only by the *im* present, Rs origin more proximal, and R5 convexity not vein-like.

EOPTYCHOPTERININAE Lukashevich, subfam. n.

Diagnosis. Stout insects with short antennae, flagellomeres covered with numerous small setae. Wing broad, costal space widened. *sc-r* just beyond proximal Rs origin. Both Rs against M fork and R4+5 at *r-m* angulate backwards, distal Rs aligned rather with R2+3 which is nearer to R1. *r-m* before R4+5 midlength, joining *d* cell near midlength. M stem weak, often untraceable. *im* before M1+2 fork, M3+4 simple. CuP near base (sub)angulate at *cu-a*, 1A distad of the latter reduced. Alular incision deep, alula sometimes produced.

The only genus included: *Eoptychopterina* Kalugina, 1985.

Age. Early Jurassic to Early Cretaceous.

Alinkidae

This monobasic Triassic family was assigned to Asilomorpha (without further discussion of its relationships) as synapomorphic with other groups of the infraorder in very long R4+5 stem (Krzeminski, 1992c). Remaining wing characters of *Alinka* Krzeminski, however, don't agree with those of the most generalized brachyceran families (their character states given in parentheses), namely Rhagionidae and Xylophagidae s.l. (both known since the Jurassic; the latter including *Protobrachyceron* Handlirsch):

(1) *sc-r* halfway from *h* to Sc apex (in basal position);

(2) Rs originating just before M fork (well before),

(3) Rs forking well beyond M fork (level with it) and nearly level with *r-m* and Sc apex (before both),

(4) Rs aligned with R4+5 (not so), straight at *r-m* (bent);

(5) *r3* cell narrow like *r1* one (at least as broad as *r5* one);

(6) *m-cu* proximal (more distal), joining CuA at its midlength (far beyond) and M3+4 near base (M3+4 close to fork, or M4).

From both the oldest Rhagionidae (such as *Palaeobrachyceron* V.Kovalev), considered the most primitive Brachycera, and their presumed ancestors, Protorhyphidae (Séguy, 1951), the *Alinka* is distinct in further wing characters:

(7) R4+5 fork much shorter than M1+2 one (subequal);

(8) M2 base not shorter than *im* (much shorter, or M1+2 forking beyond *im*).

Short R4+5 fork, characteristic of only some groups of Asilomorpha (including Early Jurassic Oligophrynidae; Ansorge & Krzeminski, in press, a), is met with also in Mesozoic Bibionomorpha (Paraxymyiidae s.l., ?Pachyneuroidea). The characters (1), (5), (6) and (8) of *Alinka* are shared with most, and (3) and (4) with some Procramptonomyiidae (Pachyneuroidea); (2) is found in recent *Pergratospes* (Cramptonomyiidae, Pachyneuroidea; on the composition of the superfamily see below under Axymyiomorpha). The antenna of *Alinka*, with scape much shorter than pedicel (like in procramptonomyiids) and 8-segmented flagellum not tapered towards obtuse apex, has no counterpart among Asilomorpha known (either flagellum subulate, or scape longer). The female cerci are 2-segmented, like in both Procramptonomyiidae and most lower Brachycera. In fact, the only significant difference of *Alinka* from procramptonomyiids is the short R4+5 fork, and it seems much more logical to consider Alinkidae an aberrant member of Pachyneuroidea, possibly descending from Procramptonomyiidae and ancestral to Paraxymyiidae. Therefore, at present the Brachycera are still unknown from the Triassic.

SYSTEM AND PHYLOGENY

ON THE ORIGIN OF DIPTERA

Groundplan of dipteran wing

The most generalized of Triassic Diptera known, Vladipteridae, give us a possibility to reconstruct the groundplan dipteran wing on the more sound basis than before. Some earlier reconstructions were reproduced by Krzeminski (1992c: Fig. 12a—c), and the characters not matching with (or not specified in) all of them are given in **bold**.

Wing rather small, elongate, without dark pattern. Sc close to R, half wing length or somewhat longer. ***sc-r* just beyond or before Rs origin** (never terminal). R kink noticeable in horizontal plane. R1 long. Rs originating at 1/3 wing length or slightly beyond, straight, forking (rather symmetrically) somewhat distad of M fork into R2+3 and R4+5. R2+3 very long, **short oblique R2 entering margin close to R1.** *r-m* joining R5 base or short R4+5 to *d* cell before midlength. Strong convex M base diverging from R, M stem **somewhat desclerotized**, forking symmetrically just before wing midlength, *d* cell long. **M1+2 forking well beyond *im*. M3+4**

rather long, forking about *m-cu*. Both R5 and M4 slightly convex, unlike R2-4 and M1-3. CuA nearly straight at *m-cu*, curved backwards near apex, **entering margin about 2/3 wing length**. Concave iCu along convex CuA well developed, not reaching margin. CuP subparallel to CuA, concave throughout. Convex 1A about half of CuA, reaching margin. **2A free and short.** No alular incision.

All the primitive wings of Diptera are distinct from any oligoneurous Mecoptera in the following combination of apomorphic characters:

(1) clavus flat with weak veins, therefore complex CuA developed (in fact, concave CuA s.str. secondarily released from convex M5), and

(2) costal+subcostal space narrow, with deeply concave Sc usually close to R-R1, the latter straight at Rs origin (both C+Sc-R+ and CuA+iCu-CuP forming stiff spars; Wootton & Ennos, 1989);

(3) R kinked just beyond humeral level (Riek, 1977), strongly convex M base diverging early from R;

(4) R5 distinctly convex;

(5) CuA curved backwards near apex;

(6) wing base narrow, 3A lost, 2A short;

(7) crossveins of submarginal series (other than *im*) lost (except for some preserved in few genera of Tipulomorpha and Tanyderidae), and only discal and proximal crossveins retained: *h*, *sc-r*, *r-m*, *m-cu*, *cu-a*, and *ia*; two latter shifted basad, and *icu* lost.

The MA mentioned as significant dipteran apomorphy (Wootton & Ennos, 1989; Willmann, 1989a) is still not formed as vein-like structure in a number of primitive recent Nematocera. The R kink opposed to the arched base of M (MP) stem appeared earlier in dipteran evolution.

Mecopteran ancestors

The Diptera are believed to be descendants of the extinct mecopteran suborder, Paratrichoptera (= Protodiptera = Mesopsychina; Crampton, 1925: 54, etc.). The group was first created for Triassic Mesopsychidae (Tillyard, 1919a) as an order combining forewing characters of Mecoptera (3 free claval veins, simple CuA) and Trichoptera (both Rs and M dichotomously 4-branched). Later the group was included into Mecoptera as a suborder (Martynova, 1959) and used as 'waste-basket' for various aberrant families. Now the Paratrichoptera are discarded as polyphyletic (Novokshonov, 1993b). Leaving aside the **Pseudopolycentropodidae** (Triassic — Jurassic; 5 branches of M, forewing Sc shaped like in hindwing of Nannochoristidae) and **Mesopsychidae** itself (hindwing very similar to forewing in size and venation, Sc with several veinlets to C), we consider in more detail Liassophilidae (= Laurentipteridae = Pseudodipteridae; Triassic and Jurassic), Permotipulidae, Robinjohniidae, and Permotanyderidae (all Permian).

Forewings of four above families are similar to Diptera in having costal+subcostal space narrow (but Sc not close to R, except for *Liassophila* Tillyard), R-R1 straight at Rs origin (if the latter rather distal), and (except for Permotanyderidae) wing base narrowed with 2A lost. In **Liassophilidae** and **Permotanyderidae** (and in Pseudopolycentropodidae as well) the forewing is subtriangular and hindwing small (both evidently coupled in flight like in some Trichoptera), in contrast to fore- and hindwing of similar size and structure (probably uncoupled in flight) in **Robinjohniidae** and possibly also in **Permotipulidae**. Two latter families seem to be closely related (Novokshonov, 1993b) and have further characters in common with generalized Diptera: R2 short or (Permotipulidae) absent, M proximally fused to CuA for a distance, M4 slightly convex (uncertain in *Robinjohnia* Martynova), (M5+) CuA curved backwards near apex, and claval area rather flat with weak veins. *Robinjohnia* possess two more presumable synapomorphies with Diptera: R4+5 short, and R5 slightly convex (in contrast to R2+3 and R4; visible in the left forewing of the holotype, better at the photo published by Riek (1968)). Other derived characters shared with Diptera are found in Permotipulidae only: M+CuA fusion short, submarginal crossvein series reduced. R kink used by Riek (1977) for redefining the Diptera is rather shallow in Robinjohniidae, undeveloped in Permotipulidae, and best pronounced in Permotanyderidae (considered by him as four-winged dipterans), however, in the latter family the forewing (demonstrating also incipient free MA base) still retains large clavus with three convex veins (Willmann, 1989a).

Permotipulidae (2 Late Permian genera known by isolated wings only) described as ancient tipuloid (s.l.) Diptera (Tillyard, 1929) are now regarded as members of the Diptera stem-group (Willmann, 1989a; Wootton & Ennos, 1989). However, in permotipulids (unlike the dipteran groundplan) both R kink and R2 are absent, and R5 neutral like nearby veins (Willmann, 1989b; Novokshonov, 1993b). The claval area seems modified, and veins posterior to CuA are difficult to interpret: the first is long and weakly convex, being comparable only to CuP+1A (fused at least for a distance in hindwings of Mecoptera), and the second is short and submarginal (2A?). Wing stalk is separated by slight emargination at the short vein's apex.

It could be hypothesized that permotipulid wings, usually interpreted as fore, are actually the hind ones (Novokshonov, 1993b), but (M5+)CuA is mainly concave (with anterior convex component weaker than posterior concave) in hindwings of all the other Permian Mecoptera, including *Robinjohnia* (as visible at both published photos). The possible exception is the Permian *Minusinia* Novokshonov assigned to Robinjohniidae and known by the incomplete (probably hind) wing, with R2+3 fork as short as in *Robinjohnia* hindwing (Novokshonov, 1994a). If all known wings of Permotipulidae and *Minusinia* are **hindwings** with CuA convex (like in post-Paleozoic Choristidae, Bittacidae, Panorpidae and Panorpodidae, probably always due to wings tend to be narrowed; Novokshonov, 1993b), then *Minu-sinia* should be placed rather in Permotipulidae on account of this important synapomorphy (and could be annectent between two families). In the case permotipulids cannot be ancestral to Diptera, so far as in the latter the complex M5+CuA — was most probably transferred onto forewing from hindwing (see below). If these are **forewings**, then CuP+1A fusion is unique to Mecoptera. The fusion occurs (in much lesser degree) in forewings of some derived Diptera, and one could assume that Permotipulidae represent one more group of two-winged mecopteran descendants, but the absence of complex cubital spar (of any origin) from their wings makes the latter supposition much less probable. The discovery of *Vladiptera*, combining all dipteran synapomorphies with claval structure much more plesiomorphic than in Permotipulidae, excludes the latter from presumed ancestors of Diptera.

The present evidence points out the *Robinjohnia* as a mecopteran nearest to Diptera. This Late Permian scorpionfly is somewhat bittacid-like (long wings with narrow bases, long legs) but retaining unmodified head (short rostrum might be developed) (Riek, 1968). It was first described in Permotipulidae (Tillyard, 1937; the family being singled out as a new order Protodiptera), then separated at family level within Eumecoptera (Martynova, 1948), subsequently transferred to Paratrichoptera and synonymized under Permotipulidae (Martynova, 1961), later included in Nannochoristidae (Riek, 1968), and now considered a separate family, similar to both Nannochoristidae and Bittacidae (Willmann, 1989a) or rather to Permotipulidae (Novokshonov, 1993b). So far as true nannochoristids appeared only in the Mesozoic, one more similarity to bittacids is remarkable: R5 is convex in the latter family as well (Novokshonov, 1993a).

Both Permotanyderidae and Liassophilidae are not closely related to Diptera, representing the lineage (or rather two lineages) within Mecoptera, homoplastic in wing structure and flight mechanics with Amphiesmenoptera. Unlike them, the presumed dipteran ancestors (similar to robinjohniids) should have long homonomous wings uncoupled in flight, and the transformation of hindwing into balancing organ in the Diptera became possible only due to initially uncoupled condition. In contrast to Diptera, the ancestral coupling device is retained in two-winged male coccids (Homoptera): halter-like hindwing provided with hamuli grasping the marginal fold of forewing.

Hindwing features of dipteran forewing

Generalized broad-based forewings retain the claval supporting zone, serving as protective dorsal covering in repose, whereas the uncoupled hindwings and narrow-based forewings (both having clavus flexible) are often provided with cubital spar (Wootton, 1981). In insects having synchronous flight power-muscles (e.g. *Panorpa* and other Mecoptera), the forewing pitch and camber during stroke cycle are under muscular control (through the mutual position of costal and claval supporting zones), and the ventral bending along nodal line at the beginning of upstroke allows the distal wing part to twist to a more favourable angle of attack (Ennos & Wootton, 1989). In Diptera with power-muscles asynchronous (i.e. contracting with frequency higher than that of motor nerve impulses) the wings undergo ca. 110° twisting and camber reversal between halfstrokes, and these extensive phasic changes seem to be partly passive (powered by aerodynamic and inertial forces; Ennos, 1987), partly automatic (brought about by the relative movements of basal sclerites; Miyan & Ewing, 1988), and partly still under muscular control (Wisser, 1987); ventral flexion is diminished or bears other functions (Ennos, 1989). The hindwing of *Panorpa* with pitch and camber changes largely passive may be regarded as a functionally intermediate stage (Ennos & Wootton, 1989).

Wings of Paleoptera retaining complete **corrugation** (regularly alternating convex and concave veins) correspond to a model wing with the corrugated spars diverging serially from the leading edge spar, and develop torsion and camber passively under aerodynamic loads (Ennos, 1989). In both Hemiptera and Oligoneoptera the regular corrugation is interrupted (owing to absence of separate convex MA and concave veins posterior to CuP), but could be partly restored with the narrowing of wing bases, especially in two-winged fliers. In Diptera the corrugation increases due to R5 (in fact MA2) turning convex and (M5+)CuA dissociated, becoming interrupted with iCu (concave like following CuP). The reversal of positions of distal CuP (to convex) and distal 1A (to concave) in most Oligoneura restores nearly perfect corrugation of the wing blade. Additional corrugations appear in some dipteran lineages, and the most complicated system is acquired by Deuterophlebiidae whose males spend their entire life in flight (Courtney, 1991).

Most forewing characters of Diptera are similar rather to hindwing ones of mecopteran ancestors (Fig. 44). Dissociated (M5+)CuA is known only in hindwings of Mecoptera. The wing base and costal+subcostal space narrow, Sc rather short (groundplan feature of Diptera), proximal Rs origin, free MA base, approximation of M and Cu bases, M+CuA fusion at humeral level, base of M stem arched towards incipient R kink, and shortening of 2A are characteristic of hind rather than fore wings of Mecoptera. One more possible 'hindwing' trend in Diptera is the association of CuP near base with 1A, corresponding to CuP+1A fusion in all mecopteran hindwings.

The formation of complex cubital spar (including a pair of closely set veins, convex and concave) might be a key change causing the above phenomenon. In Diptera (as well as in Homoptera Coccomorpha) the spar is formed by dissociation of (M5+)CuA, like in mecopteran hindwing, and the development of this important structure probably forces associated characters to follow the hindwing pattern, resulting in the '**transfer**' of hindwing features onto the forewing (similarly the formation of hindwing anal loop after forewing one is hypothesized in the Permian Trichoptera; Novokshonov, 1992).

Dissociation of (M5+)CuA in Diptera could be attributed to wing base narrowing and/or dipterization, so far the improvement of cubital spar seems to be correlated with both. In some Oligoneoptera with four narrow-based wings uncoupled in flight, the non-homologous complex cubital spars are formed of a pair of approximated veins: convex (M5+)CuA and concave CuP (Mecoptera: some Bittacidae and Panorpodidae), or concave MP and convex (M5+) CuA (Myrmeleontidae, Nemopteridae and some other Neuroptera). On the other side, the Coleoptera (opisthomotorous and often in fact two-winged) have broad hindwings with initially double (M5+)CuA further strengthened by the association with nearby veins: concave MP stem (e.g. in Cebrionidae, Lampyridae), or with concave MP2 (in apical field; Scarabaeoidea, Staphylinoidea) and/or convex CuP (Scarabeoidea), resulting in formation of the most complex cubital spar known (the vein homology proposed by Forbes and modified by Tillyard (1926) is followed herein as confirmed by comparative studies). Among the opisthomotorous two-winged Strepsiptera (derivative rather than sister-group of Coleoptera, according e.g. Crowson, 1981), the corresponding hindwing vein is also complex (M5+ CuA?; Corioxenidae, Halictophagidae, Myrmecolacidae, Elenchidae and Stylopidae).

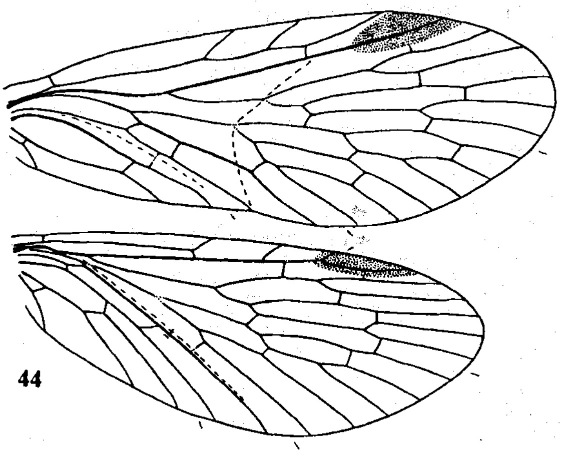


Fig. 44, *Agetopanorpa* sp. (Mecoptera, Permochoristidae; Permian), fore and hind wing venation (after Novokshonov, 1994b, schematized).

The transfer of hindwing pattern onto the forewing had possibly begun already in bittacid-like ancestors of Diptera with narrow-based wings ('copepterygous' flight type; Rohdendorf, 1949). Narrow wing stalks are considered the perfect adaptation to utilize the energy of own vortex wake during flight: being rather inactive aerodynamically, they prolong the action of beneficial dorsal vortex and delay the formation of parasitic ventral vortex (Grodnitsky & Morozov, 1993). With the reduction of hindwings to halteres in Diptera, the forewing claval region becomes secondarily expanded, partly substituting the decrease of aerofoil area. However, the expansion occurs mainly distal to wing stalk, which remains narrow, well suited for twisting (alula being bordered by incisions and never growing broader than anal lobe), and leaving enough space for beating halter (which shifted to wing base with reduction of metathorax).

Similar phenomena occurred in the evolution of Coccomorpha (Homoptera). In the extinct four-winged precoccids, the concave fold along convex (M5+)CuA is incipient (attributable to extra strengthening of the vein, supporting interalar coupling device), and forewing clavus is flat and narrow (Shcherbakov, in press). Dipterous males of true scale insects show the (M5+)CuA dissociated into convex anterior (= M5) and concave posterior (= CuA s.str.) components, and claval area usually enlarged. Their venation is extremely simplified, and only the more proximal Rs origin and loss of both M and CuA forks could be interpreted as transferred from the hindwing.

'Cranefly' habitus

Rudimentary hindwings of Diptera, the **halteres**, beat with the same frequency as the forewings, but with phase delay up to 60° (Grodnitsky & Morozov, 1993: Fig. 3C). The only other analogous structures are forewing halteres of Strepsiptera, the order descending from (or related to) Coleoptera. Dipteran halteres, bearing numerous sensillae, are considered as balancing organs maintaining the reflectory stabilization of flight course.

Some of remaining two-winged insect fliers are peculiar in having '**tails**' of various nature, which could be stabilizators of another kind (like tail of kite). Dipterous mayflies (Caenidae and some Baetidae) and Permian two-winged Palaeoptera (Permothemistidae of Megasecoptera, and Eukulojidae of Palaeodictyoptera) retain long caudal filaments (cerci and sometimes paracercus). Nemopteridae (Neuroptera) have hindwings ribbon- or thread-like. The example of male coccids is the most significant. The tails were acquired at least thrice in the infraorder: 'fleshy tassels' in Monophlebidae, waxy tuft in most other archaeococcids, and a pair of waxy rods in neococcids and their precursors; the rods were then substituted by long tail-like penial sheath in Diaspididae (Koteja, in press). All above tail-bearers belong to the taxa retaining synchronous flight power-muscles and rather low wing beat frequencies, in contrast to Diptera and Strepsiptera whose flight muscles are asynchronous (like in Coleoptera, most Hymenoptera, and some Hemiptera; Cullen, 1974; Smith & Kathirithamby, 1984).

Some opisthomotorous insects are in fact two-winged due to elytra becoming extremely short (Dermaptera, most Phasmatida, Tetrigidae, Staphylinidae) or not extended in flight (e.g. Cetoniinae), but need neither tails nor halteres. The same is true of functionally two-winged fliers with fore and hind wings mechanically coupled in flight (Hemiptera, Hymenoptera etc.). Unlike most Diptera and tail-bearers, in both latter cases the functioning wing (hind or fore+hind) has the large trailing edge region (expanded cubitoanal area of hindwing, or the whole coupled hindwing), which could absorb the inertial torques generated at the points of stroke reversal (like the flag waving after the staff). In Hymenoptera, with the increase of stroke frequency the hindwing tends to become small or even reduced (and joint wing as narrow as in Diptera), but as far as known no special organs develop for flight stabilization.

The '**cranefly**' habitus with long legs, elongate stalked wings and slender body is widespread among the Nematocera, being universal for primitive ones: all Tipulomorpha, Tanyderidae, primitive Psychodidae, most Ptychopteroidea, primitive Blephariceroidea, all Culicoidea (esp. Dixidae), primitive Chironomoidea, some Pachyneuroidea (esp. Pachyneuridae and Cramptonomyiidae), Hesperininae (Bibionidae), some Mycetophilidae (esp. Bolitophilinae), and some Anisopodidae. In light of the above considerations it seems highly probable that the flight stabilization is maintained in all these 'craneflies' not only by halteres, but by the spread legs as well. The long modified legs of some phantom craneflies (basitarsus swollen and filled by tracheae in *Bittacomorpha*) and mosquitoes (distal tibia and basitarsus plumose in *Sabethes*) are held in peculiar position during the flight and aid in its stabilization (Alexander, 1927b; Séguy, 1951: 489, and 1959: 114). The long legs seem to be inherited from the bittacid-like mecopteran ancestors whose wing bases already became narrow. Some of these extinct scorpionflies could possess also raptorial tarsi like modern Bittacidae, but the lengthening of their legs was caused by the change of wing shape rather than of preying mode. Extended legs represent one more kind of 'tails', and the retention of this method of flight stabilization (along with halteres) in lower Diptera could possibly be explained by their stroke frequency still low and function of halteres not fully developed yet.

The well-known ability of leg autotomy in craneflies is ensured in alive insect by a preformed line of weakness at trochantero-femoral junction (U-shaped sclerotized ventrobasal border of femur). Autotomy seems to be even more widespread among Nematocera than the cranefly habitus itself: the above structures are found not only in *Hesperinus*, but in *Bibio* as well, which loses its short legs easily when catched (legs are usually broken off at pleurocoxal articulation in dried specimens). The ability could be one more apomorphy of initial Diptera, so far as the U-shaped line is not formed yet in long legs used for holding prey in *Bittacus*.

Initial radiation of Diptera

Several phylogenetic classifications of Diptera were proposed. Relationships of nematoceran infraorders and Brachycera according to some of them are represented at Fig. 45. The data on wing morphology (including that of Triassic fossils) agree with the dendrogram given by Kovalev (1987), requiring only small modification of it.

The separation of Tipulomorpha (= Polyneura *sensu* Lindner, 1949) was considered the first divergence in dipteran history already by Hennig (1968), all the other infraorders being united as Oligoneura. Kovalev (1987) interpreted those of Triassic dipterans which combine both free R2 and R4+5 stalk with

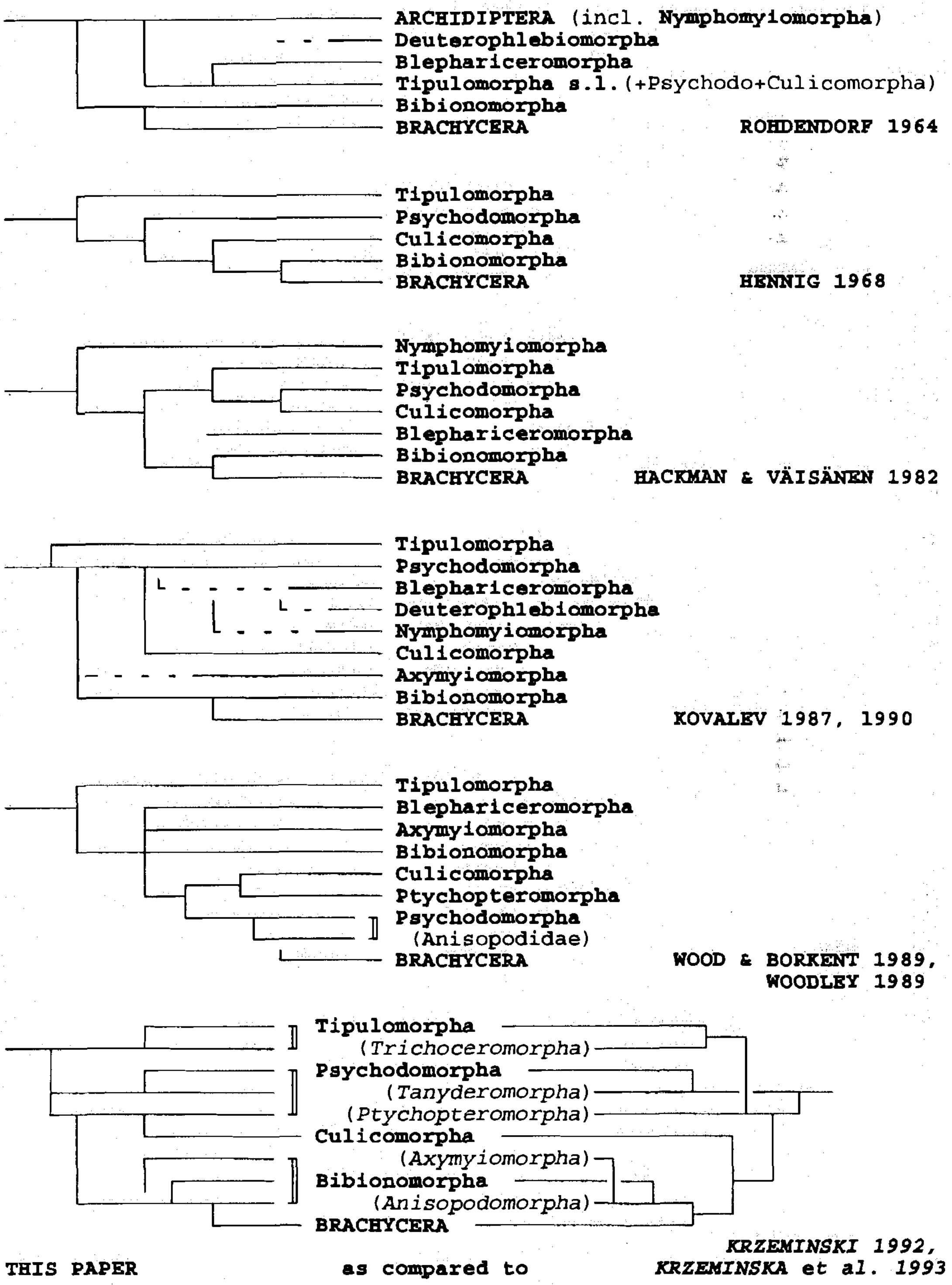


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Fig. 45. Phylogenetic relationships of nematoceran infraorders and Brachycera after different authors (schematized).

complete 1A and still undifferentiated basiala (i.e., undeveloped alular incision) as the separate family, nearest to the common ancestors of Tipulomorpha and Psychodomorpha. However, he had never actually seen the fossil exactly corresponding to the reconstruction, and not figured such a wing along with two other Triassic ones (Kovalev, 1983a: Fig. 2 is *Kuperwoodia* with R4 shown as originating from R5 and proportions 'normalized'; and Fig. 3 is *Psychotipa depicta*). Among the dipterans studied by Kovalev, *Psychotipa predicta* is nearest to the above groundplan, differing only in possessing alular incision, and the wing of *Dilemmala specula* (presumably retaining long 1A and lacking alular incision) is incomplete. The 'archetype' wing of *Vladiptera kovalevi* was collected only in 1990, three years after his untimely death, by one of us.

We prefer to include these ancestral Diptera in Tipulomorpha rather than in Psychodomorpha, regarding the formation of anal loop and separation of basiala by alular incision as more fundamental apomorphies than the apical fusion of R2 with R1. The incision is poorly developed in some Oligoneura (especially in most Ptychopteroidea), but the loop is invariably retained. The R2 becomes crossvein-like in Trichoceridae, Tipuloidea and derived Ptychopteroidea; it is lost in Blephariceroidea, Culicomorpha, Bibionomorpha, and Asilomorpha, except for some, probably aberrant specimens of Blephariceridae (R2 crossvein-like; Brodsky, 1954: Fig.1) and Vermileonidae (free; Stuckenberg, 1960: Fig.16), and an aberrant wing of Cramptonomyiidae (crossvein-like, Fig. 46), so it is impossible to ascertain whether R2 was free or not in their precursors. The latter seems more probable if we accept the hypothesis of Krzeminski (1992c) on the Ptychopteroidea (his 'Neoneura') being ancestral to Culico- and Bibiono+Asilomorpha (but not Tipulomorpha!), further supported by some wing characters. In the case, the R1+R2 fusion is a general trend within Diptera, much less weighty than the anal loop (plus alular incision), an uniquely derived character. The belonging of undifferentiated basiala to the dipteran groundplan is brilliantly substantiated by *Vladiptera*.

The only Diptera which had already acquired anal loop together with alular incision, but retained convex 1A reaching margin, are Triassic Psychotipinae, probably reflecting an incipient stage of basiala differentiation. They stand nearest to the base of Oligoneura phyletic lineage and should belong rather to Psychodomorpha if cladistic methodology to be followed, but are retained in paraphyletic Tipulomorpha, so far as complete 1A is more convenient and easily recognizable character than the loop and incision. Their wing proportions, R5 convexity and CuP course are rather tipuloid than ptychopteroid.

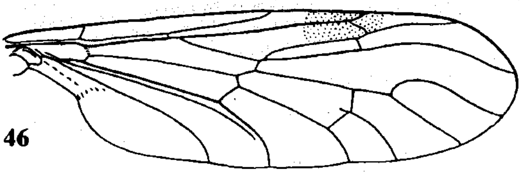

Fig. 46, *Haruka elegans* Okada (Cramptonomyiidae; Recent), aberrant venation with crossvein-like R2 present (right wing of male specimen: Kyushu, Mt. Hikosan, Fukuoka, 23.4.1975; T. Saigusa leg.; Natural History Museum, London).

However, the Rs nearly aligned with R4 (*Psychotipa*), or M1+2 forking before *im* (*Dilemmala*, provisionally assigned to Vladipterinae), both characters resembling those of Tanyderidae, could argue for Psychotipinae being already Psychodomorpha, ancestral to both psychodoid-blephariceroid and ptychopteroid lineages.

One more apomorphic character opposing Oligoneura to Tipulomorpha is a reduction of arolium replaced with flap-like empodium (Hennig, 1968; Röder, 1984, cited in Oosterbroek & Theowald, 1991). The Trichoceridae and Limoniidae seem to be peculiar (apomorphic?) among the Diptera and other Oligoneoptera studied in the male genitalia developing partly from pupal ectoderm (entirely from imaginal discs in Anisopodidae; Dahl, 1980).

Psychodoidea and Blephariceroidea, synapomorphic in 1A joining Cu, constitute one of two main lineages within paraphyletic Psychodomorpha (Mesozoic Ansorgiidae partly fill the gap between these two superfamilies), and couldn't be ancestral to remaining groups of Oligoneura. This lineage is still not recorded, but should be represented in the Triassic (possibly with psychodoids more primitive than Tanyderidae), like its presumed sister-group, Ptycho-pteroidea (with most generalized Nadipteridae). Enigmatic Hennigmatoidea demonstrate a mosaic of characters, apomorphic ones being shared chiefly with Nadipteridae, their probable relatives.

Several similarities in larval mouthparts of Tanyderidae and especially of Ptychopteridae to Culicomorpha, as well as the loss of ocelli in adult, were interpreted by Wood & Borkent (1989: 1341, 1359) as synapomorphies uniting both these families, or rather the latter one, with Culicomorpha. This assumption seems to be further supported by some adult characters shared with Culicomorpha: mesothoracal mediotergit enlarged in relation to pleurotergit in *Ptychoptera* (Crampton, 1926), CuP angulate near base in Eoptychopterinae and Ptychopteridae, and somewhat mosquito-like habitus with wings and body pilose in *Eoptychoptera*. However, Eoptychopteridae are more apomorphic than Culicomorpha at least in the structure of CuP, so the Eoptychopterinae + Ptychopteridae lineage is rather parallel than ancestral to that infraorder, which possibly could be derived from nadipterid-like precursors. Culicomorpha are apomorphic in the R4 forming common stalk with R(2+)3, the state unknown in Ptychopteroidea (but universal in Hennigmatidae) and widespread among Psychodoidea and Blephariceridae. However, the character seems to be of little importance, being highly homoplastic: stalk appearing in Trichoceridae, usually more than once within Vladipteridae, Tipuloidea, Tanyderidae, Psychodidae, Blephariceridae, and probably thrice within Bibionomorpha (see below).

The pronounced nodal flexion line and complete desclerotization of M stem of another eoptychopterid subfamily, Eoptychopterininae, are characteristic rather of Bibionomorpha, and R5 angulate at *r-m* in similar manner is known in Axymyiidae, whose larvae resemble (at least habitually) most closely just ptychopterid ones (running to the same couplet in the key; Teskey, 1981: 126). Considering these wing similarities rather homoplastic, we suggest that Bibionomorpha might have arisen from early ptychopteroids in a similar way. Therefore, at present Nadipteridae seem closest to ancestors of both Culico- and Bibionomorpha.

The main novelty suggested by Kovalev (1987) in his dendrogram, the independent and heterochronous derivation of both Culicomorpha and Bibionomorpha (the latter ancestral to Brachycera) from Psychodomorpha, seems quite convincing. The only presumed synapomorphy of Culico+Bibionomorpha (Hennig, 1968), pulvilli, is not found in most culicomorphan families. The basiala structure is entirely different in these two infraorders, being highly apomorphic in Culicomorpha. Both the absence of Culicomorpha from the Triassic assemblages, and only 3 families recorded in the Early Jurassic ones (compared to 4 and 9 families of Bibiono+Asilomorpha, respectively) agree well with the assumption about the later separation of Culicomorpha. Culicoidea and Chironomoidea are known since the Early Jurassic; among the former, a new dixid genus is similar to chironomoids in R3 joining R1 and could be close to their ancestors (Lukashevich, in press, b). The Bibionomorpha diverged into Pachyneuroidea and Anisopodoidea already by the Late Triassic, and Asilomorpha descended from Anisopodoidea (Crampton, 1925; Woodley, 1989), namely, from Protorhyphidae (Séguy, 1951), by the Liassic. A possible synapomorphy of most Bibionomorpha with Brachycera is introduced herein, radial+anal hair plates; Axymyiidae and Perissommatidae, both lacking these plates, could constitute the first branch from bibionomorph stem (see below).

In the phylochronogram proposed (Fig. 47), Tipulomorpha, Psychodomorpha and Bibionomorpha are paraphyletic ancestral taxa. The modified system of Nematocera is summarized in the Table 2.

On some infraordinal concepts

PSYCHODOMORPHA *sensu* Wood et Borkent

Since the recognition of striking similarity between Trichoceridae and Anisopodidae in larval (Keilin, 1912) and adult thoracal structure (Crampton, 1925), these and some other families were often considered as retaining dipteran groundplan characters (Edwards, 1926) and representing the extant assemblage nearest to initial Diptera ('trichocerid-anisopodid complex' of Krivosheina, 1969). Recently, Wood & Borkent (1989) interpreted the above larval similarities as synapomorphic and grouped Trichoceridae (traditionally in Tipulomorpha), Psychodidae, Perissommatidae, Scatopsoidea, and Anisopodidae s.l. (three latter in Bibionomorpha) under Psychodomorpha; the concept first appeared in McAlpine et al. (1981), and the same taxa except Psychodidae were united under Anisopodomorpha by Krivosheina (1988).

As first proposed by Edwards (1926) and confirmed by Oosterbroek & Theowald (1991), these characters are absent in some members of this group and/or are present in other nematoceran taxa (e.g. Tipuloidea, Tanyderidae, Blephariceridae, Deuterophlebiidae, Thaumaleidae, Axymyiidae) as well, so they are rather symplesiomorphies. For example, larval mandibles operating in oblique or subvertical planes and/or bifold ('two-segmented', often shaped like spider's chelicerae) are clearly apomorphic, if compared to simple chewing ones moving in the same horizontal plane in opposition to one another (as in other insects), and apparently associated with feeding on particles in (semi)liquid medium (Wood & Borkent, 1989). This character polarity is confirmed by the shift from horizontal to subvertical movement during larval development in Cylindrotomidae (Oosterbroek & Theowald, 1991). But this unusual condition, found in a number of primitive forms in each infraorder (e.g. in Ptychopteridae and Rhagionidae, besides above-mentioned), most probably belongs to the dipteran groundplan (Anthon, 1943), and all the exceptions are due to either ontogenetically preceding condition being restored, or the membrane between the two parts of mandible becoming secondarily sclerotized (as in blephariceridae larvae during maturation; Courtney, 1991).

The taxa in question have no wing or other adult characters in common, belonging to at least four

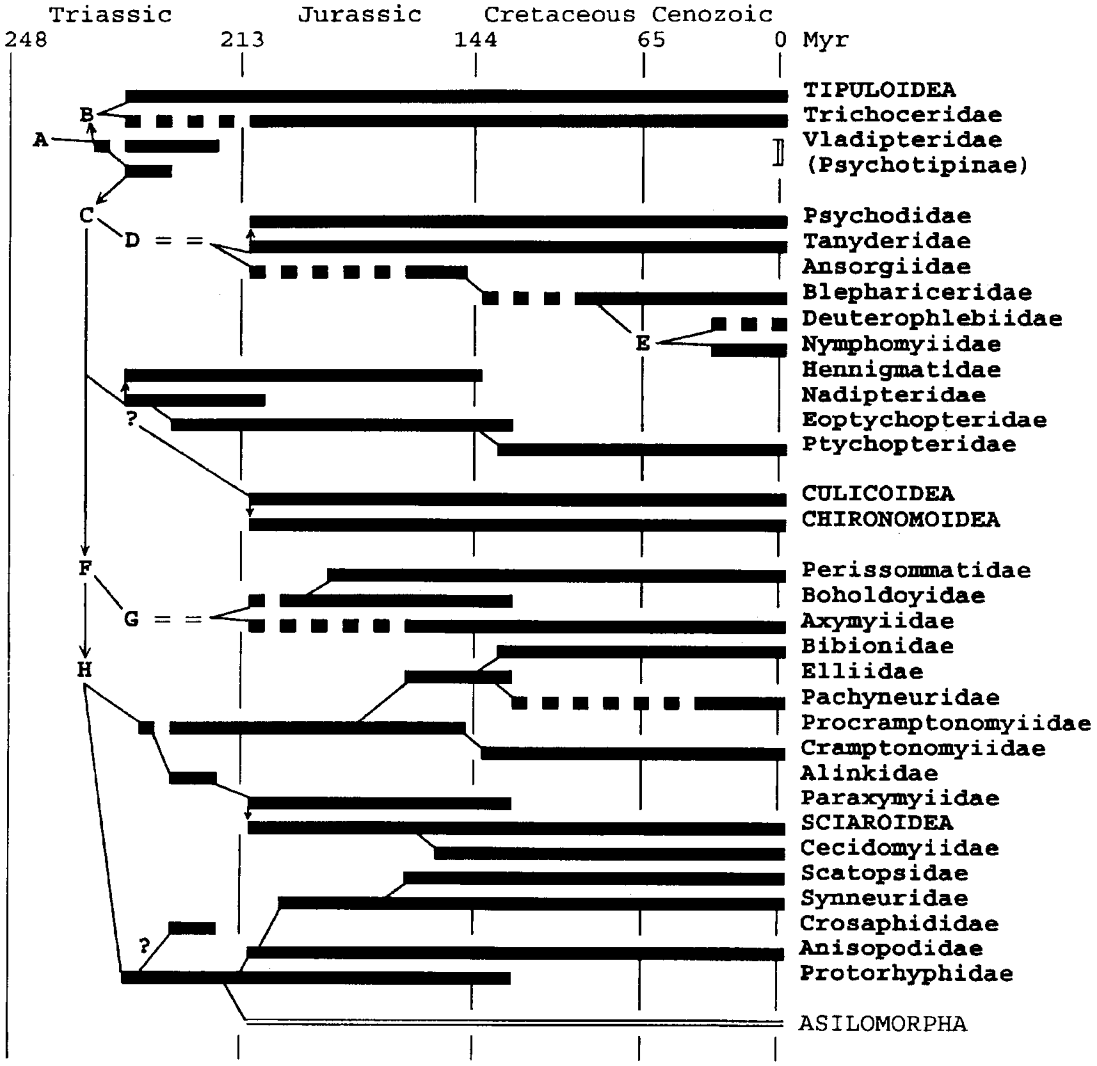

Fig. 47. Phylochronogram of Nematocera.

Apomorphies other than in wing structure mainly after Wood & Borkent (1989), non-homoplastic in **bold**. Apomorphies are listed for each internode (marked with capital letter) or for each taxon (for paraphyletic taxa marked with *, synapomorphies with descendent taxa). Hypothetical age of families (inferred from phylogeny, but not confirmed yet by fossil record) in broken line.

A, DIPTERA (*TIPULOMORPHA and ***Vladipterinae** have no apomorphies of their own): Preradial space narrow, R stem kinked, R2+3 fork short, R4+5 fork very long, R5 convex, **(M5+)CuA dissociated and curved backwards distally**, clavus reduced (2A short, 3A lost), submarginal crossvein series tends to be reduced, **hindwing transformed into halter, pro- and metathorax very reduced**; (extrapolated from extant groups of Tipulo- and Psychodomorpha) **labium modified into proboscis, 8th abdominal spiracle lost in male,** pupa with adherent appendages, **larva** legless **with bifold mandibles operating in oblique planes**.

B: R2 joining R1, M stem tends to align with M3+4, 2A very short and submarginal, mandibles lost, **male genitalia developing partly from pupal ectoderm**.

Trichoceridae (TRICHOCEROIDEA): 1A shortened (but reaching margin).

TIPULOIDEA: *sc-r* tends to be terminal, ocelli and free cardo lost; larva metapneustic with head retractile.

***Psychotipinae**: **anal loop and alular incision developed**, R4 tends to be captured by R3 (= R3+4 stalk formed).

C, 'OLIGONEURA' (*PSYCHODOMORPHA have no apomorphies of its own): **1A distally reduced** (not reaching margin), **R5 convexity continued basad posterior to Rs,** CuP entering margin in basal wing half; (unless in Psychotipinae) **arolium replaced with empodium.**

D: Rs aligned with R4 (*r-m* joining R5 base), *im* shifted distad of M1+2 fork, *cu-a* replaced with anastomosis, empodium setiform to absent (unless claws vestigial).

***Tanyderidae** (PSYCHODOIDEA): *sc-r* terminal, M2 convex, ocelli lost, male genitalia inverted.

Psychodidae: CuP shortened, anal lobe reduced, 2A forming marginal projection ('wing scale'), *im* usually absent, body and wing veins densely haired.

***Ansorgiidae** (BLEPHARICEROIDEA): Sc weak, antennae short, wings permanently extended at rest, **legs prehensile with long claws folding against distitarsus, male gonocoxites and 9th sternum fused into small capsule**; (possibly also) R2 reduced, **male genitalia dorsoflexed.**

***Blephariceridae**: C not continued beyond wing tip, M1+2 simple, *im* lost, **wings unfolding at emergence; larva** apneustic **with** (at least in 1st instar) **paired abdominal prolegs.**

E, Deuterophlebiidae + Nymphomyiidae: mouthparts and digestive tract atrophied, metasternum partly exposed, **femur subdivided**, abdominal spiracles vestigial, **wings deciduous** at least in female.

***Nadipteridae** (*PTYCHOPTEROIDEA): CuP strongly diverging from CuA; (extrapolated from Ptychopteridae and Culicomorpha) ocelli lost, **larva with mandibular comb and invaginated premandibular apodeme.**

***Eoptychopteridae**: R2+3 approximated to R1, R2 joining R1, M stem aligned with M1+2, *m-cu* joining base of long M3+4, CuP distally strongly convex and curved backwards from claval fold.

Ptychopteridae: *im* lost, mesopleuron lacking transepimeral suture.

Hennigmatidae: **R base weak,** Rs aligned with long R2+3+4.

***CULICOIDEA** (CULICOMORPHA): **Torsion joint at R kink, radial+axillary hair plates,** R2 lost, R3+4 stalk formed, MA vein-like and transverse, M3+4 simple, *im* lost, **Cu base tends to be captured by** *cu-a*, CuP base angled towards 1A, pedicel enlarged, (post)laterocervicale with ventromedian projection, empodium tends to be setiform; **pupa: palpal sheath curved posteromesad, hind leg sheath S-shaped and concealed beneath wing sheath**; **larva: labral brush complex, torma and premandible invaginated.**

CHIRONOMOIDEA: R3 joining R1, sperm transferred by spermatophore; **larva with prothoracal proleg and procerci.**

F, *BIBIONOMORPHA: R2 lost, M base weak to reduced.

G, 'AXYMYIIFORMIA': M3+4 simple, CuP distally reduced, eyes longitudinally subdivided, mandibles lost, palpomeres short, postcervicale lost; larva with antennae reduced and caudal siphon retractile.

Axymyiidae (AXYMYIOIDEA): R3+4 stalk formed, *im* lost; **pupa with abdominal siphon**; **larva with anal papillae very long** and mandibles moving horizontally.

***Boholdoyidae** (PERISSOMMATOIDEA): Sc distally reduced, **pterostigma distad of short R1,** ambient vein continued beyond wing tip.

Perissommatidae: R3+4 stalk formed.

H, radial+anal hair plates, M1+2 fork shifted basad to near *im*; (unless at F) chiasmata lost at meiosis in male.

***Procramptonomyiidae** (*PACHYNEUROIDEA, 'BIBIONIFORMIA'): M base oblique, pedicel slightly enlarged, mandibles lost; larval mandibles moving horizontally.

***Elliidae**: R3+4 stalk formed, fore tibiae tend to be fossorial.

Bibionidae: R3+4 simple; **larva with intersegmental fissures interrupted and displaced laterally.**

Pachyneuridae: M3 and *im* lost.

Cramptonomyiidae: R4 fused to R3 except base.

***Alinkidae**: R4+5 fork short.

***Paraxymyiidae**: M3 and *im* lost.

***SCIAROIDEA**: R4+5 simple, meron greatly reduced, 2 spermathecae; pupal leg sheaths coplanar (not superposed); larva: cardo tends to be fused to cranium, metathoracal spiracle lost.

Cecidomyiidae (CECIDOMYIOIDEA): flagellomeres with encircling setal rows, tibial spurs lost; **larval head tiny with stylet-like mandibles.**

***Protorhyphidae** (*ANISOPODOIDEA, 'ANISOPODIFORMIA'): *sc-r* basal, MA vein-like and oblique, **M base along Cu base,** CuP base tends to be associated with 1A.

***Anisopodidae**: Rs with 2 branches, mandibles lost, pulvilli (but not empodium) reduced; **larval hypostomal bridge lost.**

Crosaphididae: M3 and *im* lost.

***Synneuridae** (SCATOPSOIDEA): (unless in mycetobiine-like ancestors) M3 and *im* lost; M1+2 fused to Rs for a distance; (in recent members) larval head greatly reduced.

Scatopsidae: M fork shifted basad, palpus one-segmented.

***ASILOMORPHA** (BRACHYCERA): CuA converging with CuP distally, 8 flagellomeres, palpus 2-segmented; larval head partly retracted.

Table 2. Modified system of Nematocera

			Age	First find reference
Tipulomorpha				
	Vladipteroidea			
		Vladipteridae	T2/3-T3	this paper
	Trichoceroidea			
		Trichoceridae	J1-R	*Krzeminski (1992b)
	Tipuloidea			
		Limoniidae	T2/3-R	this paper
		Tipulidae	K1/2-R	Krzeminski (1992a)
		Cylindrotomidae	P1/2-R	Freiwald (1991)
Psychodomorpha				
	Psychodoidea			
		Tanyderidae	J1-R	Ansorge (1994)
		Psychodidae	J1-R	Ansorge (1994)
	Blephariceroidea			
		Ansorgiidae	J3	Krzeminski& Lukashevich (1993)
		Blephariceridae	K2-R	*Kovalev (1987)
		Deuterophlebiidae	R	
		Nymphomyiidae	N1-R	*C.Hoffeins (pers. comm.)
	Hennigmatoidea			
		Hennigmatidae	T2/3-K1	this paper
	Ptychopteroidea			
		Nadipteridae	T2/3-J1	this paper
		Eoptychopteridae	?T3-K1	Krzeminski (1992c)
		Ptychopteridae	K1-R	Kalugina (1989)
Culicomorpha				
	Culicoidea			
		Dixidae	J1-R	Lukashevich (in press, b)
		Chaoboridae	J1-R	Lukashevich (in press, b)
		Culicidae	K2-R	*Poinar (1992)
	Chironomoidea			
		Thaumaleidae	J3(?)-R	Kovalev (1989)
		Chironomidae	J1-R	*Ansorge (1994)
		Ceratopogonidae	K1-R	*Schlee & Dietrich (1970)
		Simuliidae	J3(?)-R	Kalugina (1991)
Bibionomorpha 'Axymyiiformia'				
	Perissommatoidea			
		Boholdoyidae	J1(?)-K1	Kalugina & Kovalev (1985)
		Perissommatidae	J2-R	Kalugina & Kovalev (1985)
	Axymyioidea			
		Axymyiidae	J3-R	*this paper
'Bibioniformia'				
	Pachyneuroidea			
		Procramptonomyiidae	T3-J3	Krzeminski (1992c)
		?Alinkidae	T3	Krzeminski (1992c)
		Elliidae	J3-K1	Krzeminska et al. (1993)
		Cramptonomyiidae	K1-R	Blagoderov et al. (1993)
		Pachyneuridae	P3/N1-R	*Schlee & Glöckner (1978)
		?Paraxymyiidae	J1-K1	*this paper
	Bibionoidea			
		Bibionidae	K1-R	*Kovalev (1987)
	Sciaroidea			
		Mycetophilidae s.l.	J1-R	this paper
		Sciaridae	K1-R	*Kovalev (1984)
	Cecidomyioidea			
		Cecidomyiidae	J3(?)-R	Kovalev (1990)
'Anisopodiformia'				
	Anisopodoidea			
		Protorhyphidae	T2/3-K1	this paper
		Anisopodidae s.l.	J1-R	Handlirsch (1925)
		?Crosaphididae	T3	Kovalev (1983b)
	Scatopsoidea			
		Synneuridae	J1(?)-R	this paper
		Scatopsidae	J3-R	this paper

New taxa and new placements in **bold**; most of doubtful families omitted. Age: T – Triassic, J – Jurassic, K – Cretaceous, P1 –Paleocene, P2 – Eocene, P3 – Oligocene, N1 – Miocene, R – Recent. References to undescribed finds marked with *.

distinct basiala types (Trichoceridae to the most generalized of extant types, and Anisopodidae to the most derived among Nematocera). Their larval symplesiomorphies were preserved due to similar ecology: for example, larvae of *Perissomma fusca*, along with those of *Sylvicola*, Scatopsidae, Psychodidae, Trichoceridae etc., dwell in the liquefied (autodigested) macromycetes (Colless, 1962), and all the 'Psychodomorpha' *sensu* Wood et Borkent could be found in a single mushroom. Therefore, this infraordinal concept should be abandoned.

Blephariceromorpha

The infraorder was created along with Deuterophlebiomorpha and Nymphomyiomorpha by Rohdendorf (1964), all three subsequently united with Psychodomorpha by Hennig (1968, 1973) as probably synapomorphic in mesothoracal meron fused to epimeron. The concept was later restored and expanded to include also **Deuterophlebiidae** and **Nymphomyiidae** (McAlpine et al., 1981). Courtney (1991) confirmed the monophyly of the infraorder and considered it synapomorphic with Psychodomorpha *sensu* Wood et Borkent and Ptychoptero+Culicomorpha in larval mandible rotation oblique to vertical, but as shown above it is rather a groundplan feature for Diptera. We prefer to follow Hennig in retaining the group (as Blephariceroidea) within paraphyletic Psychodomorpha, because its relationship to Psychodoidea (through Jurassic Ansorgiidae) is more evident than that of Culicomorpha to Ptychopteroidea. Of three extant families included, Deuterophlebiidae are absent from fossil record, Blephariceridae are found in the Late Cretaceous (undescribed specimens mentioned by Kovalev, 1987) and Nymphomyiidae in Miocene Bitterfeld amber (C. Hoffeins, pers. comm.).

The Nymphomyiidae are shown to be highly specialized members of Blephariceroidea, possibly synapomorphic with Deuterophlebiidae in: the adult mouthparts and digestive tract atrophied, metasternum partly exposed, femur subdivided, abdominal spiracles vestigial, and (at least in female) empodium setiform and wings shed along a predetermined line of weakness (Wood & Borkent, 1989: 1348; Courtney, 1991). The family has nothing in common with the extinct Nematocera described by Rohdendorf (1961) within 'Archidiptera' from the Lower Jurassic beds (formerly considered Upper Triassic). These fossils, separated into infraorders Dictyodipteromorpha and Diplopolyneuromorpha, in fact belong to Tipulomorpha (Dictyodipteridae, Hyperpolyneuridae, Diplopolyneuridae) and Bibionomorpha (Dyspolyneuridae) (Kovalev, 1983a; Krzeminski, 1992c; Evenhuis, 1994; unpubl. data).

Axymyiomorpha

The infraorder was first separated from Bibionomorpha as monobasic (McAlpine et al., 1981; Wood & Borkent, 1989). Kovalev (1990) expanded its concept to include also Pachyneuridae, Perissommatidae and Thaumaleidae, all with anterior Rs branch forked and posterior one simple, and interpreted the branches as R2+R3 and R4+5, following e.g. Hennig, 1973 (convex R5 of Thaumaleidae was incorrectly labelled as M1 in Stone & Peterson, 1981). Similar modification of the concept (based on Rs pattern as well) was independently proposed by Amorim (1992), who added Perissommatidae and Pachyneuridae (as possessing 3 larval synapomorphies with Axymyiidae) and two Early Jurassic genera. Of these latter, *Rhaetomyia* Rohdendorf in fact belongs to Chaoboridae (Lukashevich, in press, b), and *Oligophryne* Rohdendorf (Oligophrynidae) to Asilomorpha (Ansorge & Krzeminski, in press, a). The above larval characters are unreliable: mandible lacks external tooth in Perissommatidae, spinules on abdominal tergites are widespread (also e.g. in Synneuridae and some Mycetophilidae s.l.), and tufts of setae on mouthparts are absent in Pachyneuridae but present e.g. in Anisopodidae.

The problematic **Thaumaleidae**, usually placed in Culicomorpha (e.g. Hennig, 1968), were transferred to Bibionomorpha on account of the loss of meiotic chiasmata in males (Hackman & Väisänen, 1982; shared also by Blephariceridae), asymmetry of larval spiracles, and some preimaginal plesiomorphies (otherwise unknown in Culicomorpha; Kovalev, 1989). Thaumaleids really differ from the rest culicomorphan families in the weakly costalized venation with forks shifted proximad, strong nodal line marked with vein desclerotizations, extremely short CuP and no alular incision. However, their basiala with M base strong and Cu base captured by *cu-a* is typical for Culicomorpha, and R3 joining R1 is characteristic of Chironomoidea, whereas the R joint is more developed than in any Bibionomorpha. Besides the larval synapomorphies of Chironomoidea (prothoracal proleg, procerci; Wood & Borkent, 1989), the significant adult (postcervicale with mesoventral prolongation, anepisternal cleft very broad and deep — Crampton, 1925; radial+ axillary sensory plates) and pupal (S-shaped hind leg sheath concealed beneath wing sheath — Hennig, 1973; palpal sheath curved posteromesad) synapomorphies of Culicomorpha are shared by Thaumaleidae. Therefore the traditional placement of the family is accepted herein.

Kovalev's concept of Axymyiomorpha was used by one of us, and the family **Elliidae** (2 genera; Late Jurassic — Early Cretaceous), combining the above Rs pattern with M 4-branched and *im* retained, was described as representing the initial superfamily within the infraorder and descending from **Procramptonomyiidae** (2 genera; Late Triassic — Late Jurassic); the Rs branches were interpreted as R3+R4 and R5 (Krzeminska et al., 1993). The latter homology seems much more reliable, because *Polyanka* Krz., Blag. et Krz. (Elliidae) is very similar to *Procramptonomyia* V.Kovalev (occuring in the same locality) in all the respects, except for the R4 being but approximated to R(2+)3 in the latter and forming stalk with it in the former.

Moreover, the extant **Cramptonomyiidae** (Lower Cretaceous *Pivus* Blag., Krz. et Krz. and 3 recent genera; Blagoderov et al., 1993; Upper Jurassic *Tega* Blag., Krz. et Krz. doesn't belong here), which have two simple Rs branches proximally connected by a transverse veinlet, and M 4-branched with *im* retained, are otherwise similar to extant *Pachyneura* (in larval and adult characters, especially male genitalia) enough to be included in Pachyneuroidea (Krivosheina & Mamaev, 1970; Blaschke-Berthold, 1994) or sometimes even in **Pachyneuridae** s.l. (as a subfamily; Wood, 1981b). Both above Rs patterns are derivable from the same groundplan condition, common to Mesozoic Protorhyphidae and Procramptonomyiidae (three long branches, R(2+)3, R4 and R5), by either proximal (Elliidae, Pachyneuridae) or distal (Cramptonomyiidae) fusion of R3 with R4. A crossvein-like R2 recorded in one aberrant wing of recent cramptonomyid (Fig. 46) agrees with the assumption.

The homology of three main Rs branches with R(2+)3, R4 and R5 through all the Diptera (Hennig, 1954) is further supported by R2 never being very long when four Rs branches retained (except for derived Psychodoidea), including all Triassic forms and Ptychopteroidea (possibly ancestral to both Bibiono- and Culicomorpha).

Besides the Cramptonomyiidae and Elliidae, the Late Triassic **Alinkidae** (Krzeminski, 1992c) are probably derivable from Procramptonomyiidae and could be included in **Pachyneuroidea** (= Ellioidea, **syn. n.**). Recent pachyneuroids resemble Bibionidae s.l. (including Hesperininae and Pleciinae) in larval and genital structure (Wood, 1981b). The fossorial fore tibiae with strong apical spur (like in some Bibioninae) are found in *Ellia* Krz., Blag. et Krz., and the difference between stout *Ellia* and slender other pachyneuroids parallels that between typical **Bibionidae** and *Hesperinus*. Both venation patterns found in bibionids are derivable from *Ellia*-like one (but with R3+4 already simple) through the loss of either *im* (Hesperininae, Pleciinae) or M3+4 base and R3+4 (Bibioninae; the crossvein retained is rather *im* than M3+4 base, M3+4 appearing as anterior branch of CuA); the common ancestor of both bibionid subgroups **should** have the discal cell closed. The Sc, always long in pachyneuroids and bibionids, often becomes shorter in other lineages of Bibionomorpha. In the phylogeny published by Blaschke-Berthold (1994), the Pachyneuroidea+Bibionoidea are united by three synapomorphies in the structure of larval antennae and mouthparts, and opposed to Sciaroidea+Cecidomyioidea. If the Bibionidae are really derivable from the ancestors with R4 fused to R3 (in contrast to Sciaroidea where it fused rather to R5), it could be better to include Pachyneuroidea in Bibiono-idea.

One more Mesozoic family presumably allied to pachyneuroids, **Paraxymyiidae** s.l., equals Eoplecioidea (Kovalev, 1990) minus *Eoplecia* Handlirsch (in fact belonging to Anisopodidae s.l.; Ansorge & Krzeminski, in press, b), and is recorded since the Early Jurassic (undescribed) until the Early Cretaceous (*Eomycetophila* V. Kovalev). Paraxymyiids are similar to Alinkidae in retaining free and sometimes very short R4, but in the *im* lost, M 3-branched and other characters agree with primitive **Sciaroidea**. It seems possible to derive the latter superfamily from Procramptonomyiidae via Alinkidae and Paraxymyiidae. Besides **Sciaridae**, the superfamily comprises paraphyletic **Mycetophilidae** (in the broadest sense), usually treated as a series of closely related extant families. Mesozoic family-group sciaroid taxa (beginning with Protopleciidae known since the Early Jurassic) are likewise close to some of the extant ones, and all of them are conventionally mentioned together as Mycetophilidae s.l. in the Table 2.

The family **Axymyiidae** itself (Axymyioidea; undescribed Late Jurassic fossils and 3 recent genera) was originally separated at infraordinal level on account of numerous larval and pupal autapomorphies (Wood & Borkent, 1989), but the action seems unjustified until the reliable synapomorphies of Bibionomorpha *sensu restricto* revealed. Axymiids were pointed out as particularly resembling **Perissommatidae** (Middle Jurassic *Palaeoperissomma* V.Kovalev and one recent genus; Kalugina & Kovalev, 1985) in the adult structure: longitudinally subdivided eyes, absence of postcervicale, (at least incipient) V-shaped suture, deep anepisternal cleft, long wing with R4 proximally fused to R3 and *r-m* joining R5 (Colless, 1962), and short palpomeres (Amorim, 1992). An undescribed recent female specimen was mentioned as intermediate between these families (Hennig, 1973; Wood, 1981a). Despite the entirely different larval habitus, two similarities occur: caudal siphon present (Amorim, 1992) and at least slightly retractile; antennae reduced. The ambient vein continued onto hind margin in

Perissommatidae is probably a reversal, like in Cecidomyiidae.

As shown by Kovalev (Kalugina & Kovalev, 1985; Kovalev, 1990), the problematic **Boholdoyidae** (2 genera, Early (?) Jurassic — Early Cretaceous) are similar to perissommatids in the short antenna with pedicel larger than nearby segments, long neck lacking postcervicale, complete V-shaped suture of mesonotum, deep anepisternal cleft, ambient vein continued onto hind margin, both Sc and CuP reduced distally, R1 short (pterostigma distad of it, if developed), wings unproportionally long, and eyes divided into dorsal and ventral components (two latter features are not characteristic of the second genus, *Daiamyia* V.Kovalev). However, he interpreted the above similarities as homoplastic due to posterior, not anterior, Rs branch being forked in boholdoyids. Taking in account the above homology of Rs branches, we consider boholdoyids as members of **Perissommatoidea**, probably ancestral to perissommatids (like Procramptonomyiidae to Pachyneuridae).

If the absence of radial+anal hair plates in Axymyiidae and Perissommatidae is primary, these two families (together with Boholdoyidae) might represent the earliest side branch from bibionomorph stem, which separated before the acquisition of hair plates (and divergence of Pachyneuroidea and Anisopodoidea) and should be eventually found in the Triassic. They are treated herein as a section **'Axymyiiformia'**, in addition to **'Bibioniformia'** (including Sciaroidea and Cecidomyioidea) and **'Anisopodiformia'**, informal taxa proposed by Hennig (1954, 1973).

Anisopodomorpha

The infraorder was separated from Bibionomorpha by Tuomikoski (1961) for **Anisopodidae** s.l. (including Mycetobiinae; of other two subfamilies, at least Olbiogastrinae since the Liassic) and Mesozoic **Protorhyphidae**. Late Triassic *Crosaphis* Evans was redescribed as related to *Mycetobia* (Kovalev, 1983b), but its position remains doubtful. (Peculiar *Valeseguya* described in Mycetobiinae (Colless, 1990) is similar rather to Sciaroidea in basiala structure, as figured for amber species (Grimaldi, 1991); its venation is derivable from that of Ditomyiinae.) Hennig (1954) considered *Cramptonomyia* as a member of Anisopodoidea and placed Mycetobiidae near Sciaroidea due to M3 and *im* retained in two former and lost in two latter; Anisopodoidea *sensu* Hennig are based exclusively on symplesiomorphies. The difference in M pattern between *Mycetobia* and Anisopodidae is the same as between *Pachyneura* and Cramptonomyiidae.

A sister-group relationship of Anisopodoidea to remaining Bibionomorpha was inferred on account of adult characters (venation, mouthparts, male genitalia, position of abdominal spiracles; Tuomikoski, 1961) and further confirmed with larval morphology (more primitive in Anisopodidae than in Pachyneuroidea and related groups; Krivosheina & Mamaev, 1970), adult prothorax structure (two different apomorphic trends; Krivosheina & Zaitsev, 1982) and basiala construction (synapomorphic in Anisopodoidea and Brachycera). The pachyneuroid lineage is traceable back with Mesozoic Procramptonomyiidae up to the Late Triassic *Yala* Krzeminski (already demonstrating both pedicel and male genitalia somewhat enlarged unlike anisopodids), and anisopodoid one with Mesozoic Protorhyphidae up to Triassic *Vymrhyphus*.

The Hennig's concept of the higher taxon based on Anisopodidae was used earlier by one of us (Blagoderov et al., 1993) for the 'plesion' easily recognizable by wings and including Procramptonomyiidae and Cramptonomyiidae (but not Elliidae). The above evidence seems sufficient to prefer Tuomikoski's concept.

Somewhat bibionid-like **Scatopsoidea** are now often placed between Perissommatidae and Anisopodidae on account of larval similarities (which are symplesiomorphic — see above). The striking resemblance of perissommatid larvae and pupae to scatopsid ones was pointed out by Colless (1962). However, the true anepisternal cleft (anterior to prealare and basalar pit) of perissomatoids and axymyiids is not homologous to the cleft, running along pleural suture in scatopsoids, anisopodids and bibionids (both clefts are present e.g. in chironomid *Diamesa* — Crampton, 1925: Fig. 41). Moreover, the radial+anal hair plates, undeveloped in Perissommatidae and Axymyiidae, are clearly defined in scatopsoids and anisopodids. Two latter groups are synapomorphous in the larval hypostomal bridge lost (Wood & Borkent, 1989) and possibly also in pulvilli (but not empodium) reduced. Therefore one could assume that the Scatopsoidea are remote descendants of Anisopodidae, and include the superfamily provisionally in a section 'Anisopodiformia'. Of two scatopsoid families, **Synneuridae** (= Canthyloscelididae) are known since the Early (?) Jurassic (Kalugina & Kovalev, 1985; besides *Prohyperoscelis* V. Kovalev, also *Mesoscatopse* V. Kovalev included on account of long R1, forked Rs, and two spermathecae), and **Scatopsidae** (?= Protoscatopsidae) since the Late Jurassic.

We retain paraphyletic Bibionomorpha in the broad sense, as well as paraphyletic Psychodomorpha s.l., instead of splitting both (separating e.g. Ptychopteromorpha, like in Krzeminski, 1992c) and devaluing ordinal rank taxa. The three sections of Bibionomorpha may correspond rather to superfamilies of other infraorders, and more extensive and detailed study is needed to elucidate their composition and interrelationships.

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