

A REVIEW OF EXTINCT MESOZOIC GENERA
AND FAMILIES OF BRACHYCERA
(INSECTA, DIPTERA, ORTHORRHAPHA)

BY AKIRA NAGATOMI & DING YANG

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ABSTRACT

The present paper was inspired by the work of Evenhuis (1994) who catalogued the fossil Diptera. The Mesozoic Brachycera are discussed here through the illustrations and descriptions of previous authors, but the taxa re-evaluated are limited to extinct families, extinct genera of Stratiomyidae, Rhagionidae and Rhagionempididae, and the genera as yet not satisfactorily assigned to an established family. The Zhangsolvidae is erected as a new family. The Apsilocephalidae (including 3 living genera) is treated as a new junior synonym of Rhagionempididae. The results are summarized in Tables 1-3 (pp. 156, 158).

[For amendment to Stratiomyoidea and Nemestrinoidea, see APPENDIX I (p. 160) & II (p. 162) and Tables 5-7 (p. 162).]

INTRODUCTION

Ideally all of the fossil taxa of Brachycera should be discussed. However, regrettably they are limited to the following: Mesozoic taxa; extinct families; extinct genera of Stratiomyidae, Rhagionidae and Rhagionempididae (= Apsilocephalidae), genera unplaced in a proper family; taxa included in Evenhuis (1994); and Kovalev's gen. et sp. 1 and gen. et sp. 2 questionally placed in Rhagionidae by him (1986) [these 2 genera are not mentioned in Evenhuis (1994)]. No re-evaluation is made here of even extinct genera of Nemestrinidae, Acroceridae, Bombyliidae (Mythicomyiinae), Asilidae, Empididae and Cyclorrhapha which include the following genera questionally placed by Evenhuis (1994): Nemestrinidae, Ussatchev, 1968 (Upper Jurassic); Empididae, *Empidia* Weyenbergh, 1869 (Upper Jurassic), *Hasmona* Giebel, 1856 (Upper Jurassic) and *Retinitus* Negrobov, 1978 (Upper Cretaceous).

This paper is a by-product of "The Chinese species and the world genera of Vermileonidae" now in preparation by Nagatomi, C. Yang & D. Yang. It was intended initially to clarify the fossil taxa which are possibly related to Vermileonidae. This work follows from Evenhuis (1994) who catalogued the fossil Diptera known up to that time, and the citation format follows him under each taxon name.

Keys 1-3 to the living families (except Nemestrinoidea, Asiloidea, Empidoidea and Cyclorrhapha) based on wing characters have been made for re-evaluation of the fossils. Keys 2-3 each present a broad picture and exact measurements are necessary for a number of taxa where exceptional cases may occur.



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No fossil specimen has been examined directly and the notes on each taxon in this paper are based on the assumption that the original illustrations reproduced are accurately drawn.

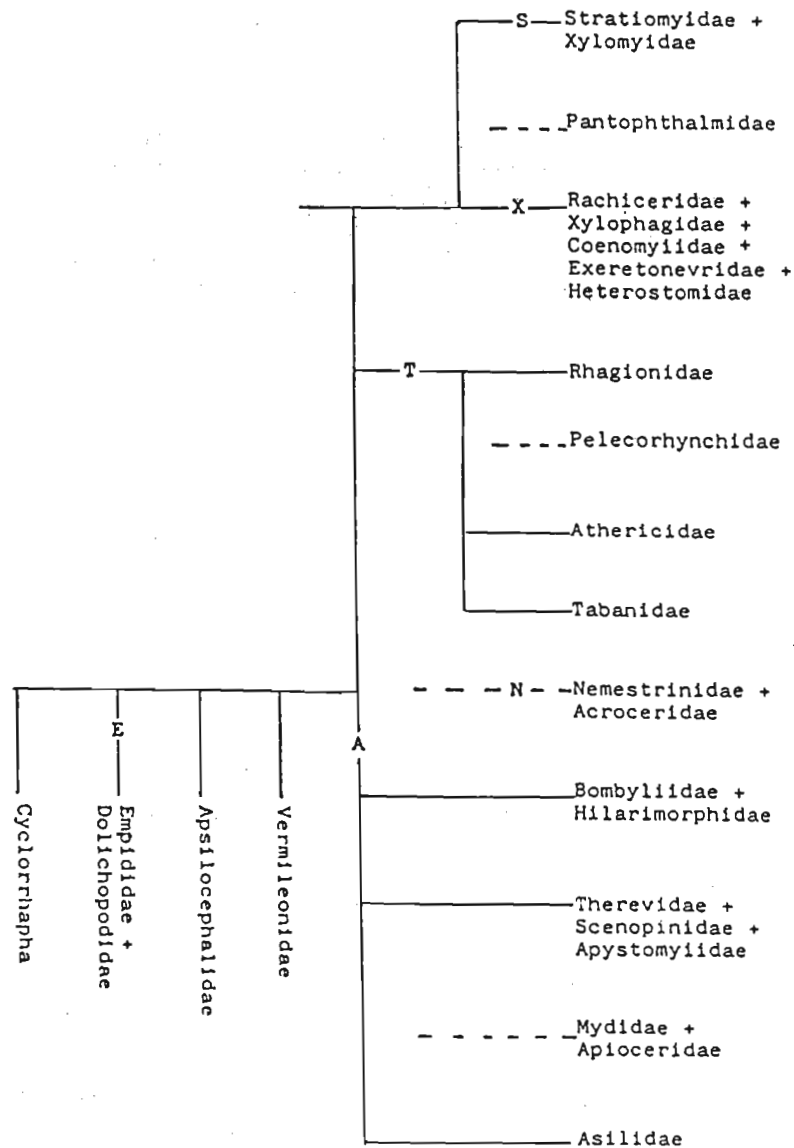
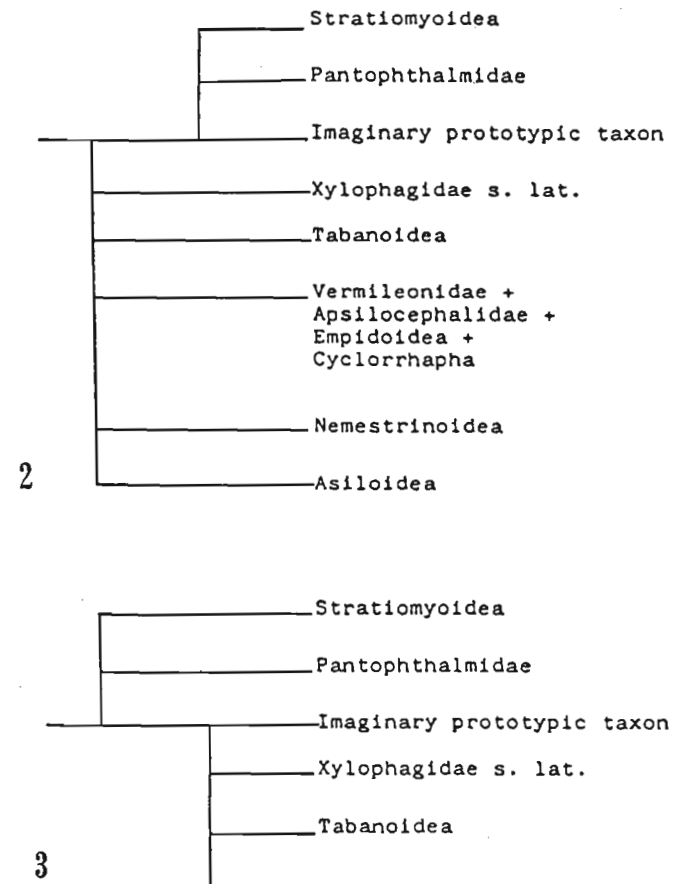


Fig. 1. — Possible phylogenetic tree of orthorrhaphous Brachycera. A, Asiloidea; E, Empidoidea; N, Nemestrinoidea; S, Stratiomyoidea; T, Tabanoidea; X, Xylophagoidea. From Nagatomi (1996).



Figs 2-3. — Most plausible phylogenetic trees of orthorrhaphous Brachycera. From Nagatomi (1996).

A possible phylogenetic relationship among the families of the orthorrhaphous Brachycera is taken from Nagatomi (1996) and is shown in figs 1-3.

Carpenter (1992) and Hennig (1954) should be consulted as a general treatise on fossil insects or the wing venations of fossil Diptera. Ross & Jarzembowski (1993) showed the age of each family of the fossil Diptera.

As a sequel to this paper we hope in the future to make a re-evaluation on the Mesozoic Brachycera not discussed here, especially those published since Evenhuis (1994).

KEY 1: LIVING FAMILIES OF STRATIOMYOIDEA, PANTOPHTHALMIDAE, XYLOPHAGOIDEA, TABANOIDEA AND VERMILEONIDAE BASED ON WING CHARACTERS (PARTLY BASED ON NAGATOMI, 1981, 1982).

- 1 Vein R_5 ends far before wing apex 2
 — Vein R_5 ends at, very near or after wing apex 3
- 2 One or two submarginal cells present; 4th posterior cell (when present) open; alula well developed; (some species of *Ptiolina* [Rhagionidae] may fall in this branch exceptionally) Stratiomyidae
 — Three submarginal cells present; 4th posterior cell closed; alula vestigial Exeretonevridae
- 3 Mouth of 2nd submarginal cell wide and usually longer than vein R_5 4
 — Mouth of 2nd submarginal cell narrow and usually shorter than vein R_5 6
- 4 Fourth posterior cell wide open (except for some Tabanidae); alula well developed 5
 — Fourth posterior cell closed or narrowly open; alula vestigial Vermileonidae [*Leptynoma* (*Leptynoma*)]
- 5 Vein A_1 straight; anal cell closed Tabanidae
 — Vein A_1 sinuate; anal cell open Pelecorhynchidae (*Pelecorhynchus*)
- 6 Vein R_5 ends at or very near wing apex 7
 — Vein R_5 ends far below wing apex 20
- 7 Four posterior cells present (or discal cell [when present] with 3 veins and without vein M_4 from 2nd basal cell) 8
 — Five posterior cells present (veins M_3 and M_4 both complete) 13
- 8 Discal cell absent 9
 — Discal cell present 10
- 9 Mouth of marginal cell longer than that of 1st submarginal cell; discal cell always absent *Litoleptis*
 — Mouth of marginal cell not longer than that of 1st submarginal cell; discal cell usually present *Bolbomyia*
- 10 Anal cell narrowly open or closed at or just before wing margin 11
 — Petiole of anal cell long *Austroleptis*
- 11 Vein R_{2+3} curved at apical portion; often 5 posterior cells present 12
 — Vein R_{2+3} straight; always 4 posterior cells present *Bolbomyia*
- 12 Anal lobe rather angular at postero-proximal part (often complete or incomplete vein M_3 present) *Spaniopsis*
 — Anal lobe gently curved at postero-proximal margin (usually discal cell present) *Spania*
- 13 Fourth posterior cell closed or markedly convergent apically 14
 — Fourth posterior cell wide open 16
- 14 Vein R_{2+3} ends very near apex of R_1 15
 — Vein R_{2+3} ends far beyond apex of R_1 Xylomyidae
- 15 Alula vestigial; wing rather wide; 1st submarginal cell wide Rachiceridae
 — Alula well developed; wing rather narrow; 1st submarginal cell narrow Heterostomidae
- 16 Anal cell narrowly open or petiole of anal cell (when present) short; 5th posterior cell markedly wider apically 17
 — Petiole of anal cell conspicuously long; 5th posterior cell parallel-sided apically *Alloleptis*
- 17 Alula well developed; 2nd basal cell roughly as long or somewhat longer than discal cell 18
 — Alula vestigial; 2nd basal cell roughly twice as long as discal cell Xylophagidae

- 18 Vein M_4 arises from 2nd basal cell 19
 — Vein M_4 arises from discal cell *Spaniopsis*
- 19 Anal cell open *Symphoromyia*
 — Anal cell closed *Ptiolina* and *Spania*
- 20 Alula vestigial 21
 — Alula well developed 22
- 21 Fourth posterior cell divergent apically; vein Cu_1 longer and at least about $1/2$ as long as posterior section of 2nd basal cell some *Rhagio* and some '*Neorhagio*'
 — Fourth posterior cell closed, convergent or parallel-sided apically; vein Cu_1 shorter and distinctly less than $1/2$ as long as posterior section of 2nd basal cell Vermileonidae
- 22 Four posterior cells present 23
 — Five posterior cells present 24
- 23 Third and 4th posterior cell narrow (Leonard, 1930: fig. 9)
 — Third and 4th posterior cell wide (Stuckenberg, 1960: figs 72-73) Coenomyiidae (some *Dialysis*)
 — Third and 4th posterior cell wide (Stuckenberg, 1960: figs 72-73) Athericidae (some *Pachybates*)
- 24 Fourth posterior cell closed 25
 — Fourth posterior cell wide open 26
- 25 Second posterior cell convergent apically Pantophthalmidae
 — Second posterior cell divergent apically Coenomyiidae (*Dialysis*)
- 26 Vein R_{2+3} ends far beyond apex of R_1 [*Coenomyiidae* and *Atrichops* (Athericidae) may have an intermediate state and fall in both upper- and lower branch] 27
 — Vein R_{2+3} ends very near apex of R_1 32
- 27 Mouth of marginal cell much shorter than that of 1st submarginal cell 28
 — Mouth of marginal cell nearly as long as that of 1st submarginal cell Pelecorhynchidae (*Glutops* and *Pseudoerinna*)
- 28 Marginal cell not as below 29
 — Marginal cell markedly widened at subapical part *Rhagina*
- 29 Anal cell closed or convergent apically 30
 — Anal cell parallel-sided apically '*Neorhagio*'
- 30 Vein Cu_1 longer and at least about $1/2$ as long as posterior section of 2nd basal cell 31
 — Vein Cu_1 shorter and distinctly less than $1/2$ as long as posterior section of 2nd basal cell (see couplets 23, 25, 34 & 35) Coenomyiidae
- 31 Vein R_{2+3} curved upward at apical portion
 — Vein R_{2+3} almost straight at apical portion [distinction between upper and lower branch may be sometimes difficult] *Ptiolina* (part), and Athericidae (*Atrichops*)
 — Vein R_{2+3} almost straight at apical portion [distinction between upper and lower branch may be sometimes difficult] *Arthroceras*, *Arthroteles*, *Atherimorpha*, *Rhagio*, *Symphoromyia* and part *Ptiolina*
- 32 Vein Cu_1 distinctly less than $1/2$ as long as posterior section of 2nd basal cell 33
 — Vein Cu_1 at least about $1/2$ as long as posterior section of 2nd basal cell 36
- 33 Fourth posterior cell (when M_3 complete) closed 34
 — Fourth posterior cell open 35
- 34 Vein R_{2+3} distinctly shorter than vein R_1 Athericidae (*Pachybates*)
 — Vein R_{2+3} nearly as long as vein R_1 Coenomyiidae (*Dialysis*)
- 35 Section of discal cell between vein M_4 and m-cu crossvein absent or short
 — Section of discal cell between vein M_4 and m-cu crossvein markedly long Coenomyiidae (*Anacanthaspis*, *Arthropeas* and *Odontosabula*)
 — Section of discal cell between vein M_4 and m-cu crossvein markedly long Coenomyiidae (*Coenomyia*)

- 36 Anal cell open 37
 — Anal cell closed 38
 37 Anal cell narrowly open; δ costal cell normal
 Athericidae (*Dasyomma*) and *Symphoromyia*
 — Anal cell wide open; δ costal cell broad
 Athericidae (*Trichacantha*)
 38 Wing at anal lobe about as wide or wider than that at apex of Cu_1 39
 — Wing at anal lobe narrower than that at apex of Cu_1
 Schizella, *Stylospania* and *Solomomyia*
 39 Marginal cell much longer than 1st basal cell *Chrysopilus* and *Symphoromyia*
 — Marginal cell about as long as 1st basal cell Athericidae (except *Dasyomma*)

KEY 2: LIVING FAMILIES OF STRATIOMYOIDEA, PANTOPHTHALMIDAE, XYLOPHAGOIDEA, TABANOIDEA AND VERMILEONIDAE BASED ON DISTANCE FROM HUMERAL CROSSVEIN TO BASE OF Rs.

- 1 Distance between humeral crossvein and base of Rs short and not over 3 times as long as basal section of Rs Tabanoidea, part Xylophagoidea, some Vermileonidae and *Parhadrestia* (Stratiomyidae: Parhadrestinae)
 — Distance between humeral crossvein and base of Rs long and over 3 times as long as basal section of Rs Stratiomyoidea (except *Parhadrestia*), Xylomyidae, Pantophthalmidae, part Xylophagoidea and many Vermileonidae

KEY 3: LIVING FAMILIES OF STRATIOMYOIDEA, PANTOPHTHALMIDAE, XYLOPHAGOIDEA, TABANOIDEA AND VERMILEONIDAE BASED ON LENGTH OF Cu_1 .

- 1 Vein Cu_1 distinctly less than $1/2$ as long as posterior section of 2nd basal cell Xylomyidae (*Xylomya*), Pantophthalmidae, Xylophagoidea, Pelecorhynchidae (except some *Glutops*) and Vermileonidae
 — Vein Cu_1 (plus petiole of anal cell [if present]) at least $1/2$ as long as posterior section of 2nd basal cell Stratiomyidae, Xylomyidae (*Solva*) and Tabanoidea (except some genera, e.g., *Pachybatas* of Athericidae)

KEY 4: MESOZOIC FAMILIES OF BRACHYCERA (EXCEPT LIVING FAMILIES OF NEMESTRINOIDEA, ASILOIDEA, EMPIDOIDEA AND CYCLORRHAPHA) AND EXTINCT GENERA UNPLACED IN A PROPER FAMILY

[for additional taxa see Appendix I (p. 160) and II (p. 162)]

- 1 [Wing venation known] 2
 — [Wing venation unknown] 20
 2 Middle of wing not as below 3
 — Middle of wing with 2 large closed cells anastomosed with one another; (fig. 27) Palaeophoridae
 3 R veins independent of discal cell and r-m crossvein present 4
 — Part of R veins anastomosed with discal cell and r-m crossvein absent (this is probably so in *Eremochaetosoma* whose wing venation is partly not clear); (figs 19–26) Archisargidae, Eremochaetidae
 4 Vein R_5 ends far above wing apex 5
 — Vein R_5 ends at, near or far below wing apex 6
 5 Mouth of marginal cell as long as that of 1st submarginal cell; basal section of Rs conspicuously long; vein R_4 shorter than vein R_5 (it is interpreted that the apparent "upper branch" of vein R_4 represents a part of opposite wing); (eye small relative to head; antenna large; antennal segment 1 longer than wide and than segment 2; antennal flagellum longer than segments 1+2, cylindrical and bluntly pointed); (fig. 30) Protomphralidae (*Protomphrale*)

- Mouth of marginal cell much shorter than that of 1st submarginal cell; basal section of Rs less than $1/2$ as long as distance between humeral crossvein and base of Rs; vein R_4 nearly as long as R_5 (figs 86–89, 91) Stratiomyidae (*Cretaceogaster*)
 6 [Wing venation known] 7
 — [Wing venation unknown at apical portion]; (vein Sc short and mouth of subcostal cell long; mouth of marginal cell long; 4th posterior cell apparently divergent apically; vein M_4 arising from discal cell; antenna long and flagellum probably multi-segmented; empodium pad-like); (figs 106–107) *Mesostratiomyia* (probably in or near Rhagionidae)
 7 Wing venation not as below 8
 — Vein R_{2+3} with 4 (or 3 [if one vein is misinterpreted and false]) subveins; vein A_1 short and arising beyond middle of 2nd basal cell; vein R_{4+5} not branched; (vein R_{4+5} ending far below wing apex; vein Sc short and mouth of subcostal cell conspicuously wide; 4th posterior cell divergent apically; vein M_4 arising from discal cell; [presence or absence of alula uncertain]; antennal flagellum 1-segmented and with a thin arista); (figs 99–101) *Mesomphrale* (Brachycera other than Empidoidea and Cyclorrhapha)
 8 Wing not as below 9
 — Vein R_{2+3} branched (or veins R_2 and R_3 present independently); vein R_{4+5} not branched; mouth of marginal cell conspicuously wide; (vein R_{4+5} ending at wing apex; 4th posterior cell divergent apically; vein M_4 arising from discal cell; anal lobe narrow; [vein A_1 short or indistinct at apical portion]; scape and pedicel large, and flagellum distinctly 5-segmented and with apex pointed); (figs 110–112) *Stratiomyopsis* (Brachycera other than Empidoidea and Cyclorrhapha)
 9 Mouth of 2nd submarginal cell usually shorter than or at most somewhat longer than wing margin between R_1 and R_4 (or distance between tips of R_{2+3} and R_4 in some Archisargidae) 10
 — Mouth of 2nd submarginal cell much longer than wing margin between R_1 and R_4 ; (antennal flagellum with 8 segments of which each is longer than wide and last one rounded apically; mouth of subcostal cell much longer than wing margin between R_1 and R_4 ; female cercus 2-segmented and with segment 1 not dilated postero-laterally; (figs 4–6) Alinkidae (*Alinka*)
 10 Fourth posterior cell closed and with long petiole 11
 — Fourth (or 3rd + 4th) posterior cell usually wide open or sometimes nearly closed at wing margin 12
 11 Vein R_5 ends near (rather above) wing apex; basal section of Rs abruptly curved upward at base; anal cell probably closed or convergent apically; antennal flagellum 12-segmented and with short spine; ovipositor short and triangular; (figs 92–94) *Zhangsolvidae* Fam. n. (*Zhangsolva*)
 — Vein R_5 ends far below wing apex; basal section of Rs gently curved or nearly straight at base; anal cell wide open; antennal flagellum bristle-like [unless scape is overlooked] and ovipositor long and needle-like at least in *Mesosolva*; (figs 11–16) *Mesosolva* and *Prosolva* (Archisargidae)
 12 Wing margin between R_1 and R_4 much longer than mouth of 2nd submarginal cell and usually so than mouth of subcostal cell 13
 — Wing margin between R_1 and R_4 not longer than mouth of 2nd submarginal cell and much shorter than mouth of subcostal cell; antennal flagellum bristle-like [unless scape or pedicel is overlooked]; face markedly divergent apically; abdomen almost parallel-sided; (figs 7–9) *Archirhagio* (Archisargidae)
 13 Fourth (or 3rd + 4th) posterior cell long, and wide open [apart from *Ija* whose 4th posterior cell is unknown but whose alula is present]; alula present, except for *Protetmididae* [apart from several taxa whose alula is unknown] 14

- Fourth posterior cell short and convergent apically; alula vestigial; (vein R_4 short and situated opposite middle of M_1 ; anal cell convergent apically but wide open); [only wing known]; (fig. 29) Protobrachyceridae (*Protobrachyceron*)
- 14 Antennal flagellum rounded triangular and with a style pointed apically and not longer than widened base; [it is presumed that empodium is bristle-like or triangular in shape with an acute apex; tibial spurs are absent; female cercus is 1-segmented; mesonotum has several longitudinal rows of setae] 15
- Shape of antennal flagellum various but not as above [or antennal flagellum unknown] (although some living *Ptiolina* somewhat resemble members of Rhagionempididae in this character, see figs 18–29 in Nagatomi *et al.*, 1991b); [it is presumed that empodium is pulvilli-like or pad-like; tibial spurs are present; female cercus is usually 2-segmented; mesonotum usually has no longitudinal setae] 16
- 15 Anal lobe of wing gently curved (apart from Kovalev's (1986) Gen. et sp. 1 whose apical lobe is unknown); alula present at least in *Ussatchovia*; anal cell narrowly open or closed at wing margin (except for Gen. et sp. 1 having long petiole, and apart from *Rhagionempis* whose anal cell is unknown); in discal cell, posterior section (when vein M_4 arising from discal cell) shorter than apical lower section; (figs 31–36, 47–53) Rhagionempididae (5 genera)
- Anal lobe of wing angulate at postero-proximal part; alula absent; petiole of anal cell long; in discal cell, posterior section between m-cu crossvein and base of M_4 (if not M_3) longer than apical lower section; (fig. 28) Protempididae (*Protempis*)
- 16 m-cu crossvein arising from trunk of veins R_4+R_5 which is long 17
- m-cu crossvein arising from vein R_5 , and trunk of veins R_4+R_5 short; [antennal flagellum unknown]; (figs 104–105) *Mesorhagiophryne robusta* (probably in or near Rhagionidae)
- 17 [Vein A_1 known] 18
- [Vein A_1 unknown at apical portion]; (mouth of marginal cell about as long as that of 1st submarginal cell; vein R_4 ending at wing apex; vein R_5 ending far below wing apex; vein M_4 arising from discal cell); (figs 102–103) *Mesorhagiophryne incerta* (probably in or near Rhagionidae)
- 18 Vein Cu_1 longer and at least $1/2$ as long as posterior section of 2nd posterior cell; vein A_1 extending to wing margin 19
- Vein Cu_1 short and less than $1/3$ as long as posterior section of 2nd basal cell; vein A_1 ending before wing margin; [only basal part of wing known]; (figs 97–98) *Ija* (Xylophagoidea or Pelecorhynchidae of Tabanoidea)
- 19 Mouth of marginal cell distinctly shorter than that of 1st submarginal cell (except *Kubekovia* and *Jurabrachyceron*); marginal, 1st submarginal and 1st posterior cells without crossveins; (figs 54–85) Rhagionidae (11 genera)
- Mouth of marginal cell about as long as that of 1st submarginal cell; marginal, 1st submarginal and 1st posterior cells with crossveins, which may have no taxonomic significance, however; [only wing known]; (fig. 18) Eostratiomyiidae (*Eostratiomyia*) (Eostratiomyiidae is possibly identical with either Rhagionidae or Pelecorhynchidae)
- 20 Some of the characters not as below 21
- Eye small; cheek large; body and femur stout; abdomen rounded apically; last segment of antenna "bears a short apical arista in the form of a bent bristle" (after Rohdendorf, 1964); (fig. 17) Eomyiidae (*Eomyia*) (Stratiomyoidea, Xylophagoidea, Tabanoidea or Nemestrinoidea)
- 21 Either abdomen or thorax not as below 22
- Abdomen narrowed at base and widened near apical end; thorax with a lateral process behind humeral callus probably on mesonotum; (fig. 95) *Batgana* (in or near Stratiomyidae)

- 22 Abdomen tapering apically 23
- Abdomen narrowed at base; (thorax, abdomen and wing slender as in Vermileonidae; mouth of marginal cell and that of 1st submarginal cell narrow); (fig. 10) *Archisargus* (*Archisargidae*) [for correct habitus, see figs 166–167 and Appendix II]
- 23 Antennal flagellum multi-segmented and pointed apically 24
- Antennal flagellum rounded triangular and with a short style; (figs 51–53) Gen. et sp. 1 (Kovalev, 1986) (Rhagionempididae)
- 24 Hind tarsomere 2 robust and not narrower than hind tibia; (palpus 2-segmented, long and pointed apically); (figs 108–109) *Mongolomyia* (Stratiomyoidea, Xylophagoidea or Tabanoidea)
- Hind tarsomere 2 slender and narrower than hind tibia; (fig. 96) *Shulmas* (Stratiomyoidea, Xylophagoidea or Tabanoidea)

FAMILY ALINKIDAE

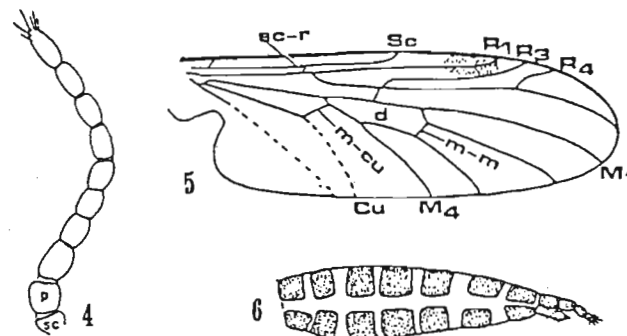
Genus *Alinka* Krzemiński, 1992, *Mitt. Schweiz. Entomol. Ges.*, **65**: 45.
Type species: *Alinka cara* Krzemiński, 1992, by monotypy.
cara Krzemiński, 1992: 46. Nearctic: USA (Upper Triassic) [Compression or impression].

This is the oldest member of the Brachycera known at present. Krzemiński (1992: 46) wrote:

"Wing length 2.3 mm, body length ab. 3.5 mm. Head partially preserved in male only, palpi invisible. ... Legs short, probably spurless. Male genital organ poorly preserved. Female genital organ presented on fig. 6c."

From figs 4–6 [= Krzemiński, 1992: fig. 6a,b,c] it is interpreted that:

tergum 10 is absent, cercus is 2-segmented, and segment 1 of cercus is not dilated postero-laterally; last antennal flagellomere distinctly longer than wide, widest around middle and rounded apically; crossvein sc-r situated before base of R_5 ; mouth of subcostal cell much longer than that of marginal cell; vein R_4 short. Its body is small. In Stratiomyoidea, Pantophthalmidae, Xylophagoidea and Tabanoidea, the body is generally larger except for some Stratiomyidae.



Figs 4–6. — *Alinka cara* Krzemiński, ♀ (Alinkidae). 4, antenna; 5, wing; 6, ♀ abdomen. sc, scape; p, pedicel. From Krzemiński (1992).

It is at once distinguished from Vermileonidae in the following points:

scape short; antennal flagellum not tapering apically; vein R_5 ending at wing apex; 4th posterior cell divergent apically; alula well developed; anal lobe developed posteroinwardly; base of vein R_{2+3} situated just beyond r-m crossvein; etc.

The Alinkidae cannot be placed in Tabanoidea because of the combination of the structure of female cercus and that of the antenna. It is easily distinguished from the Xylophagoidea by having vein Cu_1 long and not shorter than posterior section of 2nd basal cell.

In the Vermileonidae and Xylophagoidea, no definite Mesozoic fossil has been recorded.

The family Alinkidae is similar to Cramptonomyiidae (Nematocera) by having:

discal cell, sc-r crossvein, long mouth of subcostal cell, 2-segmented female cercus but is easily distinguished from the latter where antennal flagellum 13–15 segmented and vein R_4 (reaching to wing margin) absent but short r-r crossvein sometimes present.

It may be most similar to Proqramptonomyiidae with long vein R_4 but in the latter the number of segments of the antennal flagellum is probably over 10. For fossil Cramptonomyiidae and Proqramptonomyiidae, see Kovalev (in Kalugina & Kovalev, 1985), Krzemiński (1992), Blagoderov *et al.* (1993) and Krzemiński & Krzemińska (1994).

No personal study has been made here on a relation between Pachyneuridae and Cramptonomyiidae.

The family Alinkidae is at once distinguished from Anisopodidae (Nematocera) by having the following characters:

antennal flagellum 8-segmented, vein R_4 present (= vein R_{4+5} branched), female tergum 9 well developed, and female cercus 2-segmented. In Anisopodidae, antennal flagellum 14-segmented, vein R_4 absent, etc.

Peterson (1981) wrote:

"Female terminalia [of Anisopodidae] as in figs 13 and 15; cercus free and well-developed, [1-segmented], rather short in *Sylvicola* and *Mycetobia* Meigen, but often very large in *Olbiogaster*. Tergite 9 reduced, sclerotized laterally, connected ventrally with the genital fork."

Alinkidae: [Palpus unknown]; antennal flagellum clearly 8-segmented and without any modification; crossvein sc-r present.

Nematocera: The number of segments of flagellum 5–10 in Scatopsidae, 7–9 in Simulidae, 7–10 in Bibionidae and only 3 in some *Chionea* Dalman (Tipulidae), for example.

No reliable criterion is present on the number of antennal flagellar segments to establish a difference between Brachycera and Nematocera. However, the case of having an 8-segmented antennal flagellum is exceptional in Nematocera. The Alinkidae probably belongs to the Brachycera, notwithstanding the presence of crossvein sc-r. If so, it would necessarily represent an ancestral form (= stem group) of Stratiomyoidea + Pantophthalmidae + Xylophagoidea.

FAMILY ARCHISARGIDAE

Rohdendorf (1962: 334) erected a new monotypic family Archisargidae. *Archisargus* was first placed in Stratiomyidae. According to Mostovski (1996a,b, 1997), *Archirhagio*, *Archisargus*, *Mesosolva* and *Prosolva* are grouped together here as Archisargidae.

[For other genera of Archisargidae, see APPENDIX II where a key to genera is presented (p. 170).]

The 4 genera above have the following common characters:

vein R_5 ends far below wing apex; mouth of subcostal cell longer than (*Archirhagio*, *Archisargus* and *Prosolva*) or nearly as long as (*Mesosolva*) wing margin between R_1 and R_4 ; 5 posterior cells present and vein M_4 arising from 2nd basal cell; anal lobe of wing small and narrow (in *Prosolva*) or possibly so (in *Archirhagio*, *Archisargus* and *Mesosolva*); alula probably absent or vestigial; hind leg markedly long; abdomen slender, almost parallel-sided (except posterior part) or cylindrical.

The Archisargidae may have the following unique characters:

antennal flagellum would be totally bristle-like, if the scape or pedicel has not been overlooked (antennal flagellum is unknown in *Prosolva*); female abdomen has a needle-like ovipositor.

The Archisargidae is similar to Eremochaetidae in the following respects:

abdomen slender and rather cylindrical; hind leg markedly long (or probably so); mouth of marginal cell longer than (in *Archirhagio* and *Prosolva*) or nearly as long as (in *Mesosolva*) wing margin between R_1 and R_4 ; in *Archirhagio* and *Mesosolva*, antennal flagellum bristle-like totally (this is probably so in *Dissup* and *Eremochaetosoma* of Eremochaetidae).

The Archisargidae differs from the Eremochaetidae in the following points:

r-m crossvein present and any part of R veins not anastomosed with discal cell.

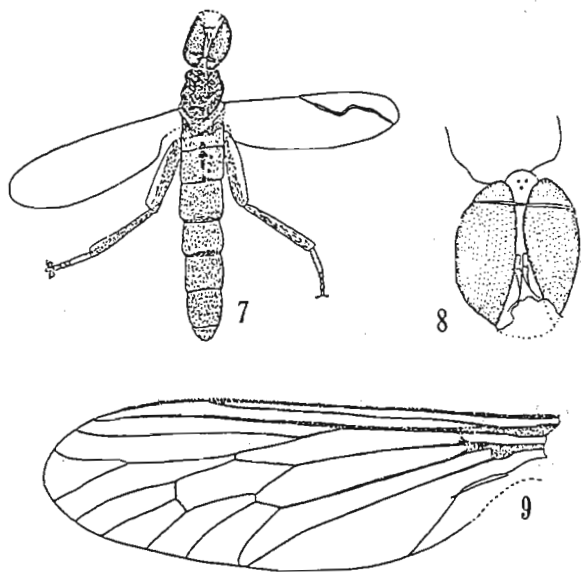
It is possible that Archisargidae + Eremochaetidae + Nemestrinidae forms a monophyletic group.

Genus *Archirhagio* Rohdendorf, 1938, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, 13(12): 35. Type species: *Archirhagio obscurus* Rohdendorf, 1938, by original designation.

obscurus Rohdendorf, 1938: 37. Palearctic: Kazakhstan (Upper Jurassic) [Compression or impression].

Body 21.5 mm and wing 13.0 mm in length. Rohdendorf (1938) put *Archirhagio* in Vermileonidae. For discussion on the position of this genus, see Hennig (1954: 369; 1967: 22–23). See figs 7–9 (= Rohdendorf, 1938: figs 6–8). Rohdendorf (1938: 59) wrote:

"An2 schwach und gebogen ... Antennen kurz und dünn; 2. Antennenglied zylindrisch, 2 $\frac{1}{2}$ –3 mal so lang als dick; 3. Glied konisch, am Ende mit dünner, nackter, ungliedeter Arista. ... [Hind leg] stark und ziemlich lang. ... Empodium gut entwickelt, kurz und breit."



Figs 7-9. — *Archirhagio obscurus* Rohdendorf, ♂ (Archisargidae). 7, body, dorsal view; 8, head, anterior view; 9, wing. From Rohdendorf (1938).

It cannot be a member of Rhagionempididae because of the presence of pad-like empodium.

It would be Vermileonidae, if a short 2nd antennal segment had been overlooked, "vein A_2 " is but a mere fold, and alula is not developed. *Archirhagio* may differ from the genera of Vermileonidae in the following points:

mouth of subcostal cell (if correctly interpreted) much longer than section of wing margin between R_1 and R_4 ; 4th posterior cell divergent apically; face markedly wider toward proboscis.

However, *Archirhagio* would be more similar to Archisargidae rather than to Vermileonidae, if antennal flagellum itself is bristle-like (scape or pedicel is not overlooked). It is distinguished from *Mesosolva* and *Prosolva* by having 4th posterior cell wide open and anal cell convergent apically.

Genus *Archisargus* Rohdendorf, 1938, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, 7(3): 30. Type species: *Archisargus pulcher* Rohdendorf, 1938, by original designation.
pulcher Rohdendorf, 1938: 30. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

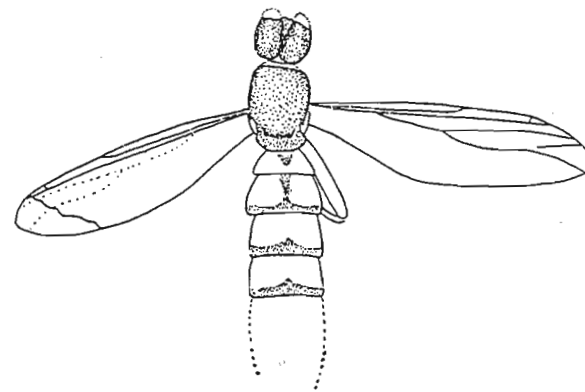


Fig. 10. — *Archisargus pulcher* Rohdendorf, ♂ (Archisargidae). From Rohdendorf (1938).

See fig. 10 (= Rohdendorf, 1938: fig. 1). Wing 16.0 mm in length. Rohdendorf (1938: 57) wrote:

"Flügel sehr lang und schmal, an der Basis stark verschmälert; ... Schildchen kurz, fast rechteckig, am Rande unbeborstet; ... Abdomen fast parallelsichtig: 1 Tergit deutlich schmaler als die anderen, vorne stark verschmälert." [Antenna, posterior parts of wing and abdomen are unknown].

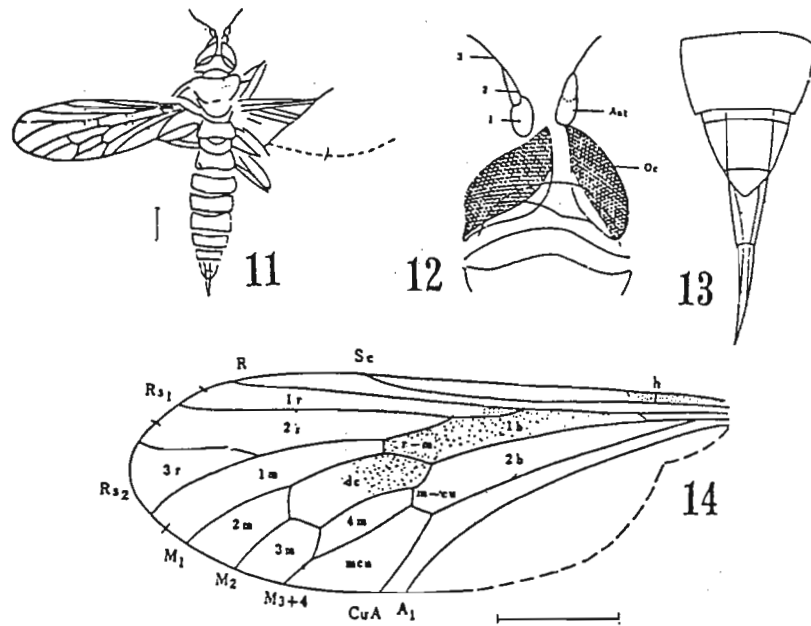
Vein R_1 is forked or subcostal cell has a short crossvein near apex, but this crossvein may be abnormal in condition. Basal section of R_s is long. Mouth of subcostal cell and that of 2nd submarginal cell respectively much longer than and nearly as long as wing margin between R_1 and R_4 . Vein R_5 ends far below wing apex. Hind leg markedly long.

However, Mostovski (1997) redescribed *Archisargus pulcher* and added a new species to this genus. See APPENDIX II (p. 165).

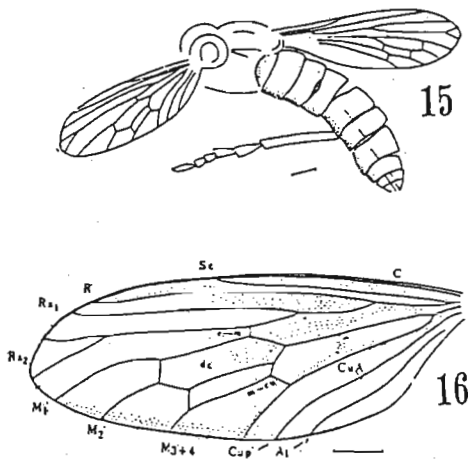
Genus *Mesosolva* Hong, 1983, *Middle Jurassic fossil insects in North China*, Geological Publ. House, Beijing, p. 133. Type species: *Mesosolva parva* Hong, 1983, by original designation.
parva Hong, 1983: 133. Palaeartic: China (Middle Jurassic) [Compression or impression].

See figs 11-14 (= Hong, 1983: figs 126a,b,c & 127).

Body 7 mm and wing 5 mm in length. Scape and pedicel longer than wide; flagellum bristle-like totally and not longer than scape + pedicel. Female frons much narrower than one eye. Mouth of subcostal cell nearly as long as wing margin between R_1 and R_4 . Mouth of 2nd submarginal cell shorter than wing margin between R_1 and R_4 . Vein R_5 about as long as trunk of R_4+R_5 . Anal cell parallel-sided apically. [Postero-proximal part of wing and detail of thorax and legs unclear.] Abdomen slender, widest around middle, and with needle-like ovipositor.



Figs 11-14. — *Mesosolva parva* Hong, ♀ (Archisargidae). 11, body, dorsal view; 12, head and antennae, dorsal view; 13, apical part of ♀ abdomen; 14, wing. From Hong (1983).



Figs 15-16. — *Prosolva huabeiensis* Hong (Archisargidae). 15, body, lateral view; 16, wing. From Hong (1983).

Genus *Prosolva* Hong, 1983, *Middle Jurassic fossil insects in North China*. Geological Publ. House, Beijing. p. 135. Type species: *Prosolva huabeiensis* Hong, 1983, by original designation.
huabeiensis Hong, 1983: 135. Palaeartic: China (Middle Jurassic) [Compression or impression].

See figs 15-16 (= Hong, 1983: fig. 128a,b).

Body 11.5 mm and wing 8.5 mm in length. [Antenna, female abdomen, detail of head, thorax and legs unknown.] Mouth of subcostal cell much longer than wing margin between R_1 and R_4 . Mouth of 2nd submarginal cell shorter than wing margin between R_1 and R_4 . Vein R_5 much shorter than trunk of R_4+R_5 . Anal cell parallel-sided apically. Vein A_2 present. Anal lobe of wing small and narrow. Alula apparently absent. Hind leg markedly long. Abdomen slender and almost cylindrical.

FAMILY EOMYIIDAE

Genus *Eomyia* Rohdendorf, 1962, *Fundamentals of paleontology*, 9: 334. Type species: *Eomyia veterrima* Rohdendorf, 1962, by original designation.

veterrima Rohdendorf, 1962: 334. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

Body 2.25 mm and wing 1.5 mm in length. Judging from fig. 17 (= Rohdendorf, 1964: fig. 80B), *Eomyia* is characterized as follows:

Eye small relative to head; cheek large; body and femur stout; abdomen rounded apically. The wing venation of *Eomyia* is not clear.

Rohdendorf (1964; 1974: 265 [English translation]) wrote,

"the antennae are two-segmented (?), the first segment is shorter and narrower than the second (?), which has the form of a bulb and bears a short apical arista in the form of a bent bristle; ..."

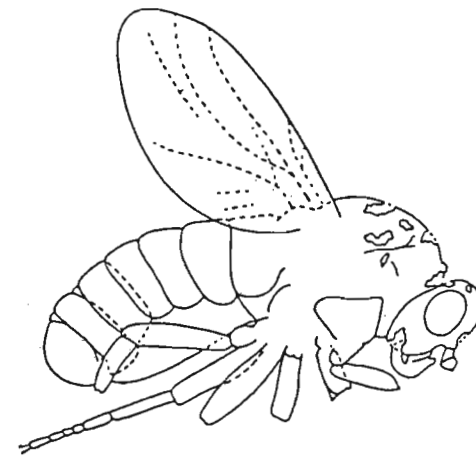


Fig. 17. — *Eomyia veterrima* Rohdendorf, ♀ (Eomyiidae). From Rohdendorf (1964).

If vein R_{4+5} ends far before wing apex, *Eomyia* would be a relative of Stratiomyidae as Rohdendorf (1962, 1964) thought. If at, near or far below wing apex, it would fall in Xylophagoidea, Tabanoidea or Nemestrinoidea.

FAMILY EOSTRATIOMYIIDAE

Genus *Eostratiomyia* Rohdendorf, 1964, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, **100**: 231. Type species: *Eostratiomyia avia* Rohdendorf, 1964, by original designation.
avia Rohdendorf, 1964: 231. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

Eostratiomyia and *avia* of Rohdendorf (1951: 79, 85; 1962: 336) are *nomina nuda* (according to Article 13 of the Code).

Wing 7.25 mm in length. In the examined specimen, marginal, 1st submarginal and 1st posterior cells have several crossveins. However, these crossveins may be abnormal and its presence may not be significant taxonomically. The wing venation of *Eostratiomyia* (fig. 18 [= Rohdendorf, 1964: fig. 80A]) would be similar to that of Vermileonidae, if the alula were absent. But it is almost certain that *Eostratiomyia* differs from Vermileonidae by having the wing more robust.

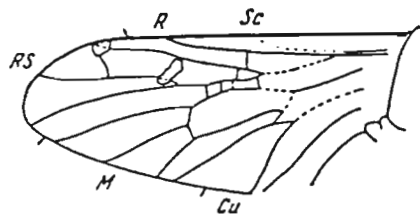


Fig. 18. — *Eostratiomyia avia* Rohdendorf (Eostratiomyiidae). From Rohdendorf (1964).

It is concluded that the wing venation of *Eostratiomyia* may easily be distinguished from that of Stratiomyoidea, Pantophthalmidae, Xylophagoidea, Nemestrinoidea and Bombyliidae (Mythicomyiinae) but would most closely resemble that of Pelecorhynchidae (*Glutops* and *Pseudoerinna*) (see lower half of couplet 27 of key 1), if the alula were present. The wing venation of Eostratiomyiidae would be identical with that of Pelecorhynchidae, if the presence of the crossveins in question and the relatively long vein Cu_1 were not significant taxonomically.

FAMILY EREMOCHAETIDAE

The taxa below are taken from Evenhuis (1994). They have the following common characters:

One or some veins of R_{4+5} , R_4+R_5 and R_{2+3} arising from discal cell; mouth of subcostal cell longer than wing margin between R_1 and R_4 (or R_{4+5}); anal cell and anal lobe of wing small and narrow; alula absent; 1st basal cell distinctly larger than 2nd basal cell; hind leg markedly long; abdomen almost parallel-sided or cylindrical and widest at segment 5.

Kovalev (1989; 1990: 101 [English translation]) wrote,

“Although I accept that the vermilionids are related to the eremochaetoids as ancestors to descendants, I must stress that the eremochaetoids deviated greatly from their ancestors because of numerous autapomorphies.”

They are similar to Vermilionidae in the following respects:

abdomen slender, clavate and widest at segment 5; hind leg markedly long; alula absent or vestigial; anal cell open.

However, they have the characters below.

(1) Wing venation: either vein R_{2+3} or R_{4+5} or both arising from discal cell (it is probably so in *Eremochaetosoma*); vein R_{2+3} ending at vein R_1 in *Dissup*, *Eremochaetus* and *Pareremochaetus*, ending just beyond vein R_1 in *Eremochaetosoma*; mouth of subcostal cell longer than wing margin between R_1 and R_4 (or R_{4+5}).

(2) Antennal flagellum: club-shaped, 6-segmented and without any arista in *Pareremochaetus*; bulb-shaped and with a longer and probably unsegmented arista (or possibly antennal flagellum itself is bristle-like as in *Mesosolva* and *Archirhagio*) in *Dissup* and *Eremochaetosoma* where it somewhat resembles that of *Vermileo* but is extremely small in size in proportion to the head; the antenna is unknown in *Eremochaetus*.

(3) Empodium (visible only in *Pareremochaetus*): “the unguitractor has two long greatly curved claws, broad pulvilli and lobiform empodium” (after Ussatchev, 1968).

(4) Female terminalia (visible only in *Eremochaetosoma*): “segment 8 together with last segment forms short conical postabdomen, ending in short spine-like ovipositor” (after Kovalev, 1989).

It is not possible to put Eremochaetidae near Vermilionidae judging from markedly different wing venation, apically rounded antennal flagellum (in *Pareremochaetus*), and needle-like ovipositor.

It cannot be placed near Bombyliidae by having the characters (2) (in *Pareremochaetus*), (3) and (4) above.

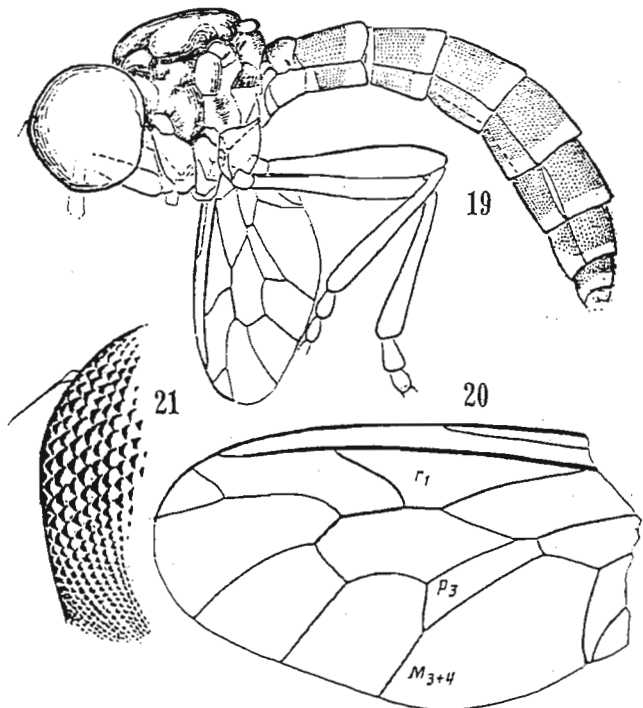
It is probable that Eremochaetidae is related to Nemestrinidae with vein R_{3+4} usually arising from discal cell; anal lobe narrow and alula absent in several genera; female cerci often “greatly lengthened, appressed to each other, and shaped like curved sabers” (after Teskey, 1981: 586); shape of antennal flagellum in some genera somewhat resembles that of *Dissup* and *Eremochaetosoma* (see Bernardi, 1973b: figs 1–13). The abdomen of Nemestrinidae (which is not slender but robust) is widest at segment 5 in some genera (e.g. *Nycterimyia*).

[For additional genera (described by Ren & Guo, 1995 and by Mostovski, 1996b) and key to genera, see APPENDIX II, p. 162.]

Genus *Dissup* Evenhuis, 1994, *Catalogue of the fossil flies of the world*, p. 316. New replacement name for *Eremonomus* Kovalev, 1989, *Paleontol. Zh.*, 1989(2): 106. Type species: *Eremonomus irae* Kovalev, 1989, by original designation. [Preoccupied by Wollaston, 1861]. *irae* Kovalev, 1989: 106 (*Eremonomus*). Palaeartic: Russia (Siberia) (Lower Cretaceous) [Compression or impression].

See figs 19–21 [= Kovalev, 1989: fig. 1a,c,d]. Body 7.5 mm and wing 3.6 mm in length. Kovalev (1989; 1989: 104 [English translation]) wrote:

“Very thin arista several times longer than third segment of antennae”.



Figs 19–21. — *Dissup* (= *Eremonomus*) *irae* Kovalev, ♀ (*Eremonomidae*). 19, body; 20, wing (except basal part); 21, anterior part of head with antenna. From Kovalev (1989).

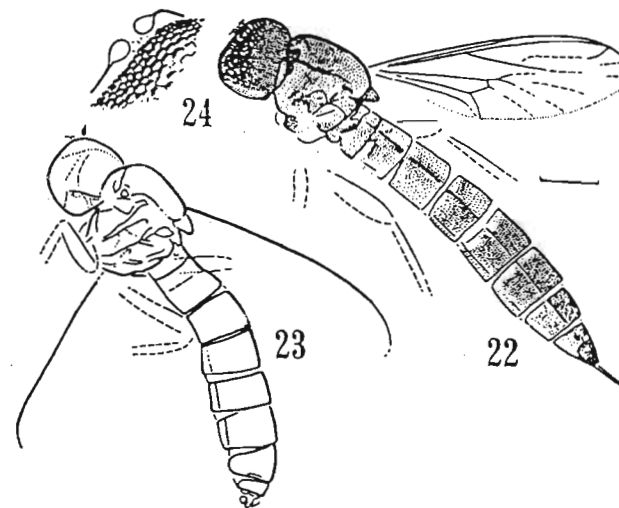
However, the scape is not visible. The flagellum would be totally bristle-like, if the widened base represents the pedicel. The antenna is conspicuously small relative to the head.

“C disappears directly after end of R_5 .” Basal section of Rs long. Veins R_{2+3} and R_4+R_5 arise from discal cell and the former ends at R_1 . Vein R_5 ends above the wing apex. Fourth posterior cell closed and with a conspicuously long petiole. Anal cell convergent apically and narrowly open. [Base of wing unknown]. Hind leg markedly long. Hind tarsomeres 1–2 widened. Abdomen long, rather cylindrical and widest at segment 5.

Genus *Eremonomus* Kovalev, 1986, *Trudy Sovmest. Sov. – Mongol. Paleontol. Eksped.*, 28: 149. Type species: *Eremonomus mongolicum* Kovalev, 1986, by original designation. *mongolicum* Kovalev, 1986: 151. Palaeartic: Mongolia (Lower Cretaceous) [Compression or impression].

See figs 22–24 [= Kovalev, 1986: fig. 120a,b,c].

Body 7.2 (♂) and 8.6 (♀) mm, wing 4.6 (♂) and 5.0 (♀) mm in length. [Wing venation is partially unknown; it is uncertain whether the last antennal segment (besides arista) represents the pedicel or a flagellum]. Antenna conspicuously small relative to head. Arista longer than elliptical widened base. Costa ends at or near wing apex. Vein R_{2+3} ends just beyond apex of R_1 . Vein R_{4+5} (if correctly interpreted) ends above wing apex and is probably anastomosed with discal cell. Hind leg probably markedly long. Abdomen long, almost cylindrical, widest at segment 5 or 6. Female abdomen with a needle-like ovipositor.



Figs 22–24. — *Eremonomus mongolicum* Kovalev (*Eremonomidae*). 22, ♀; 23, ♂; 24, antennae and eye facets. From Kovalev (1986).

Genus *Eremonomus* Ussatchev, 1968, *Entomol. Obozr.*, 47: 618. Type species: *Eremonomus asilicus*, 1968, by original designation. *asilicus* Ussatchev, 1968, *Entomol. Obozr.*, 47: 618. Palaeartic: Russia (Siberia) (Upper Jurassic) [Compression or impression].

See fig. 25 [= Ussatchev, 1968: fig. 1].

Body 11 mm and wing 5.5 mm in length. [Antenna unknown]. Vein R_{2+3} arises from 1st basal cell and ends at vein R_1 . Vein R_4+R_5 arises from the discal cell. Vein R_5 ends below wing apex. Fourth posterior cell wide open. Anal cell small and narrowly open. Anal lobe of wing small and narrow. Alula absent. Hind leg markedly long. Abdomen long, almost parallel-sided, but widest at segment 5.

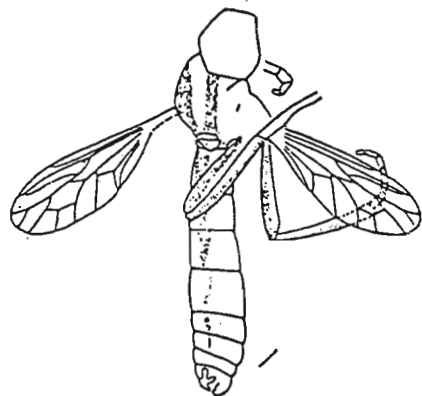


Fig. 25. — *Eremochaetus asilicus* Ussatchev, ♂ (Eremochaetidae). From Ussatchev (1968).

Genus *Pareremochaetus* Ussatchev, 1968, *Entomol. Obozr.*, **47**: 619. Type species: *Pareremochaetus minor* Ussatchev, 1968, by original designation.

minor Ussatchev, 1968, *Entomol. Obozr.*, **47**: 619. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 26 [Ussatchev, 1968: fig. 2].

Body 5 mm and wing 3 mm in length. Antennal flagellum club-shaped and 6-segmented. "Eyes touching on the vertex." Vein R_{2+3} short, arising from 1st basal cell and ending at vein R_1 . Vein R_{4+5} arising from discal cell and ending far above wing apex. Fourth posterior cell wide open. Vein A_1 incomplete and ending far before discal cell. Hind leg markedly long. Empodium pad-like. Abdomen long and almost parallel-sided.

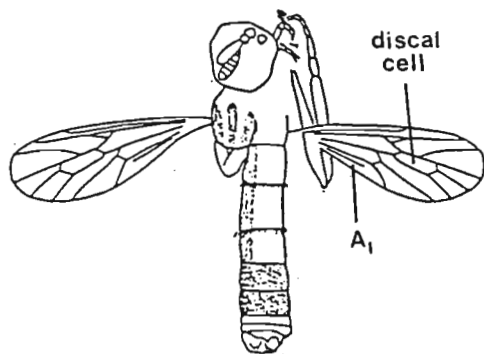


Fig. 26. — *Pareremochaetus minor* Ussatchev, ♂ (Eremochaetidae). From Ussatchev (1968).

FAMILY PALAEOPHORIDAE (= Archiphoridae)

Genus *Palaeophora* Rohdendorf, 1951, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, **35**: 106. New replacement name for *Archiphora* Rohdendorf, 1938, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, **7**(3): 41. Type species *Archiphora ancestrix* Rohdendorf, 1938, by original designation [Preoccupied by Schmitz, 1929].

ancestrix Rohdendorf, 1938: 41 (*Archiphora*). Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

Body 2.0 mm in length. Judging from fig. 27 [= Rohdendorf, 1938: fig. 13], *Palaeophora* is characterized as follows:

Head small relative to thorax; eye small relative to head; proboscis rather long (if protruded portion is truly proboscis); thorax hunchbacked (if normal in condition); abdomen robust, tapering apically, with 9 visible segments and with conspicuously long cercus; wing venation peculiar.

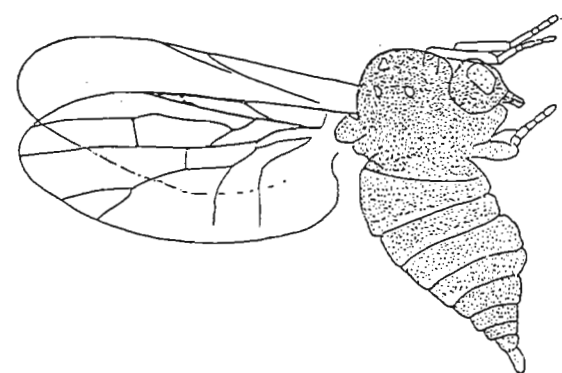


Fig. 27. — *Palaeophora* (= *Archiphora*) *ancestrix* Rohdendorf, ♀ (Palaeophoridae). From Rohdendorf (1938).

Rohdendorf (1938: 62) wrote,

"Antennen, Rüssel undeutlich, Kopfborstung wahr scheinlich fehlend. ... Beine ... unbeborstet. ... Sc fehlend; R, Rs, und Rs, stark und dick, dem Vorderrande stark genähert. ... Borsten an den Beinen undeutlich. ... ♀. Tergit mit einem Paar von Cerci."

Such a wing venation is not seen in any other families and the antenna and palpus are missing, so there is no clue even for the determination of *Palaeophora* to a suborder, i.e. Nematocera, orthorrhaphous Brachycera or Cyclorrhapha.

If the lower median closed cell is the discal cell, the venation would somewhat resemble that of Eremochaetidae, here placed in Nemes-trinoidea. The Eremochaetidae has the body longer, eye large, and abdomen slender and clavate.

There are two closed median cells anastomosed with one another in Palaeophoridae but none of them are found in Phoridae.

FAMILY PROTEMPIDIDAE

Genus *Protempis* Ussatchev, 1968, *Entomol. Obozr.*, 47: 623. Type species: *Protempis antennata* Ussatchev, 1968, by original designation. *antennata* Ussatchev, 1968: 624. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 28 [= Ussatchev, 1968: fig. 6]. Body 3.4 mm and wing 2.8 mm in length. Ussatchev (1968; 1968: 382–383 [English translation]) wrote:

Third antennal segment pyriform with a subapical stylus. Body squat. Thorax massive. Wing broad, strongly narrowed at extreme base. Vein R_5 is short. Discoidal cell present. M 3-branched. Cell cu_1 closed and on a long petiole. This family is allied to the original forms of the superfamily on the basis of antennal structures, the presence of a discoidal cell, the size of cell cu_1 , and the absence of large bristles on the legs.

Antennal stylus 2-segmented. Thorax strongly convex. Scutellum small, evenly margined. ... Anal lobe large and rectangular. Alula wanting. ... The ovipositor is of the telescopic type.

Eyes large, probably touching on vertex. The face has a distinct depression at the point of insertion of the antennae and a developed projection around the mouth margin. Vertex and occipital parts of head noticeably covered with hairs. First antennal segment as long as 2nd, together half as long as the 3rd segment. Antennal stylus more than half as long as the 3rd segment. Basal segment of stylus very short, a third as long as the apical segment, which tapers noticeably to the apex. ... Metapleura comparatively well developed. Legs with regular rows of short setiferous hairs. ... middle coxa small, with powerful bristles. ... The tibiae and all tarsal segments bear two short subapical bristles. ... C does not extend along the entire margin of the wing but ends at a fourth the distance between R_5 and M_1 on the wing margin. ... R_5 terminates slightly before the wing apex. ... The abdomen is not longer than the thorax, and it is considerably narrower than the latter. ... The two basal segments are the largest and the abdomen tapers strongly towards the apex.

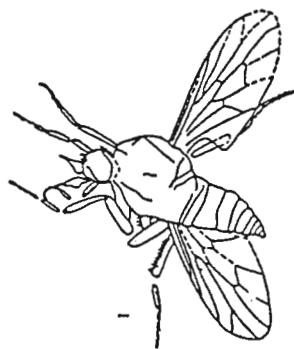


Fig. 28. — *Protempis antennata* Ussatchev, ♀ (Protempididae). From Ussatchev (1968).

The Protempididae may be separated from Rhagionempididae (= Apsilocephalidae) by having anal lobe of wing angulated at posterior proximal corner. In *Protempis*, vein M_4 (if not M_3) arises from discal cell and section of discal cell between base of M_4 and m-cu crossvein is long (vein M_3 is entirely absent). In living Rhagionempididae (with 3 genera),

vein M_4 always arises from 2nd basal cell. In *Probolbomyia* (extinct Rhagionempididae), vein M_4 arises from discal cell and its base is far distant from m-cu crossvein but alula is developed. For relation between Protempididae and Rhagionempididae, see note under Rhagionempididae.

The Protempididae is apparently more similar to Empididae than to Rhagionempididae.

FAMILY PROTOBRACHYCERIDAE

Genus *Protobrachyceron* Handlirsch, 1920, *Handbuch der Entomologie*, Band III: 205. Type species: *Protobrachyceron liasinum* Handlirsch, 1920, by monotypy.

liasinum Handlirsch, 1920: 205. Palaeartic: Germany (Lower Jurassic) [Compression or impression].

Only wing is known. See fig. 29 [= Handlirsch, 1920: fig. 179]. The Protobrachyceridae and Vermileonidae have the common wing venation:

vein R_5 ends at wing margin far below wing tip; vein R_{2+3} ends far beyond apex of R_1 ; anal cell open (but convergent apically); 4th posterior cell closed or convergent apically; 5 posterior cells present; discal cell present; alula absent or vestigial.

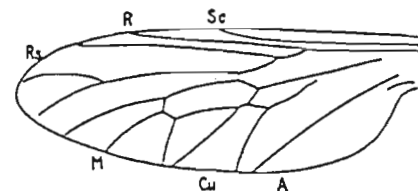


Fig. 29. — *Protobrachyceron liasinum* Handlirsch (Protobrachyceridae), wing. From Handlirsch (1920).

Vein M_4 arises from discal cell in *Protobrachyceron* and *Protovermileo* but arises from 2nd basal cell in living Vermileonidae.

It should be noted, however, that the vein Cu_1 is about $1/2$ as long as posterior section of 2nd basal cell in *Protobrachyceron* (where wing is wider) but distinctly less than $1/2$ in *Protovermileo* and living genera of Vermileonidae (where wing is narrower).

The Xylomyidae (= Solvidae) differs from *Protobrachyceron* by having the following characters: vein R_5 ends at or near wing tip; anal cell closed; alula present.

Protobrachyceron may have a kinship with Vermileonidae, although exact family identification is difficult on the basis of wing venation only, as pointed out by Hennig (1967: 3–4) and Kovalev (1981).

Protobrachyceron is placed here tentatively near Vermileonidae.

FAMILY PROTOMPHRALIDAE

Genus *Protomphrale* Rohdendorf, 1938, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, 7(3): 39. Type species: *Protomphrale martynovi* Rohdendorf, 1938, by original designation.
martynovi Rohdendorf, 1938: 40. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

Body 3.5 mm and wing 1.75 mm in length. Judging from fig. 30 [= Rohdendorf, 1938: fig. 12], *Protomphrale* is similar to Stratiomyidae and some Scenopinidae by having the vein R_5 ending far above wing apex. Its autapomorphic character is the radial sector with 4 veins but the "vein R_4 " in fig. 30 may possibly represent a margin of opposite wing. The antennal flagellum of *Protomphrale* is similar to that of *Inopus* (Chiromyzinae) and *Exodontha* (Antissini of Clitellariinae) of Stratiomyidae or *Scenopinus*, etc. (Scenopininae) of Scenopinidae. *Protomphrale* has the eye small, thorax massive and abdomen rounded apically. If pulvilliform empodium is present, *Protomphrale* would fall near Stratiomyidae. This cannot be determined but seems to be more probable. It is easily separated from Stratiomyidae by having basal section of R_s conspicuously long.

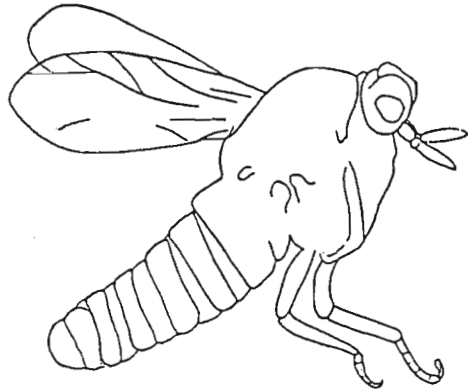


Fig. 30. — *Protomphrale martynovi* Rohdendorf (Protomphralidae). From Rohdendorf (1938).

FAMILY RHAGIONEMPIDIDAE

Apsilocephalidae Nagatomi, (A.), Saigusa, Nagatomi, (H.), & Lyneborg, 1991, *Zool. Sci.*, 8: 579. Type genus: *Apsilocephala* Kröber, 1914. **syn.n.**

Evenhuis (1994) questionably placed *Shevioptera* Kalugina (1989) in Rhagionempididae. The head and thorax are unknown, the wing venation is unclear, and the position of *Shevioptera* is uncertain.

The remaining 5 Mesozoic extinct genera have the following common characters:

- (1) antennal flagellum rounded triangular and with a style which is pointed at apex and is not longer than preceding segment;
- (2) mesonotum has paired longitudinal rows of setae (see fig. 49) in *Ussatchovia* and this is probably so in *Probolbomyia*, *Rhagionempis* and Gen. et sp. 1 of Kovalev (1986);
- (3) palpus is two-segmented in *Palaeoptiolina* and Gen. et sp. 1 and this is probably so in other 3 genera;
- (4) tibial spurs are not seen in *Palaeoptiolina* and are probably absent throughout the 5 genera;
- (5) anal lobe of wing well developed (this is unknown in Gen. et sp. 1);
- (6) alula is developed but small in *Ussatchovia* and it is so or more well developed in other genera;
- (7) two-segmented ♀ cercus is not confirmed and it is presumed that cercus is one-segmented.

The presence or absence of pulvilli- or pad-like empodium and the structure of male and female genitalia are unknown.

The wing venation of extinct Rhagionempididae (where vein R_5 ends at wing apex) most closely resembles that of *Bolbomyia*, *Ptiolina*, *Ptiolinites*, *Spania* and *Spaniopsis* of Rhagionidae (the latter 4 belong to Spaniinae) where vein R_5 (= a) is over twice (in *Bolbomyia* roughly twice) as long as distance between base of R_4 and m-cu crossvein (= b). In extinct Rhagionempididae, (a) above is shorter (in *Rhagionempis* and *Ussatchovia*) or less than twice (in *Palaeoptiolina* and *Ussatchovia*) as long as (b).

Throughout the Rhagionidae, vein R_5 is longer than the distance between base of R_4 and m-cu crossvein. However, the length of vein R_5 relative to that of the trunk of R_4+R_5 in Rhagionempididae is not significant as a familial diagnosis.

The antennal flagellum of Rhagionempididae is different in shape from that of the Spaniinae (Nagatomi, 1982: figs 5–12; Nagatomi *et al.*, 1991b: figs 18–29) as well as that of the remaining Rhagionidae.

The resemblance between Rhagionempididae and Rhagionidae becomes quite superficial, when the characters (2) and (4) above are correctly interpreted. If so, the former would belong in neither Stratiomyoidea nor Tabanoidea. The former is also easily separated from the Vermileonidae where mesonotum is without paired longitudinal rows of setae; tibial spurs 1 : 2 : 2; alula vestigial; anal lobe of wing less developed; vein Cu_1 short relative to posterior section of 2nd posterior cell; vein R_5 ending far below wing apex; etc. It is similar to Protempididae in the shape of antennal flagellum but may be different from the latter by having the anal lobe of wing not angulate, alula developed, etc.

The extinct genera of Rhagionempididae are very similar to the living genera (= Apsilocephalidae) as discussed by Nagatomi *et al.* (1991 a,b,c). No significant difference is found in wing venation and shape of antennal flagellum between *Ussatchovia* (figs 48–49) and *Clesthentiella* (Apsilocephalidae) (figs 139, 142) (Nagatomi *et al.*, 1991a: figs 27, 30). The 4th posterior cell is wide open in *Palaeoptiolina* and *Rhagionempis* but closed in *Apsilocephala* and *Clesthentiella* of "Apsilocephalidae" and in *Clesthentiella* the petiole of 4th posterior cell and that of anal cell are long.

However, if Gen. et sp. 1 of Kovalev (1986) is true Rhagionempididae and its posterolateral process on male tergum 9 represents a surstylus, the Apsilocephalidae would be identical with Rhagionempididae. We venture to treat here the Apsilocephalidae as a new junior synonym of Rhagionempididae, because it is almost certain that the latter is not Tabanoidea and contains Gen. et sp. 1 above. It has been judged that a revival of the former is low in probability. The Apsilocephalidae consisted of 3 genera: *Apsilocephala* Kröber, 1914 (1 named species from California, New Mexico, and Mexico); *Clesthertia* White, 1914 (1 named species from Tasmania); *Clesthentiella* Nagatomi, (A.), Saigusa, Nagatomi, (H.) and Lyneborg, 1991 (1 species from Tasmania).

For phylogenetic position of Apsilocephalidae, see Nagatomi (1992, 1996). It seems that Vermileonidae + Rhagionempididae (= Apsilocephalidae) + Protempididae + Empididae + Dolichopodidae + Cyclorrhapha forms a monophyletic group.

Genus *Palaeoptiolina* Kovalev, 1982, *Paleontol. Zh.*, 1982(3): 89. Type species: *Palaeoptiolina scobloi* Kovalev, 1982, by original designation. *scobloi* Kovalev, 1982: 90. Palaeartic: Russia (Siberia) (Middle Jurassic) [Compression or impression].

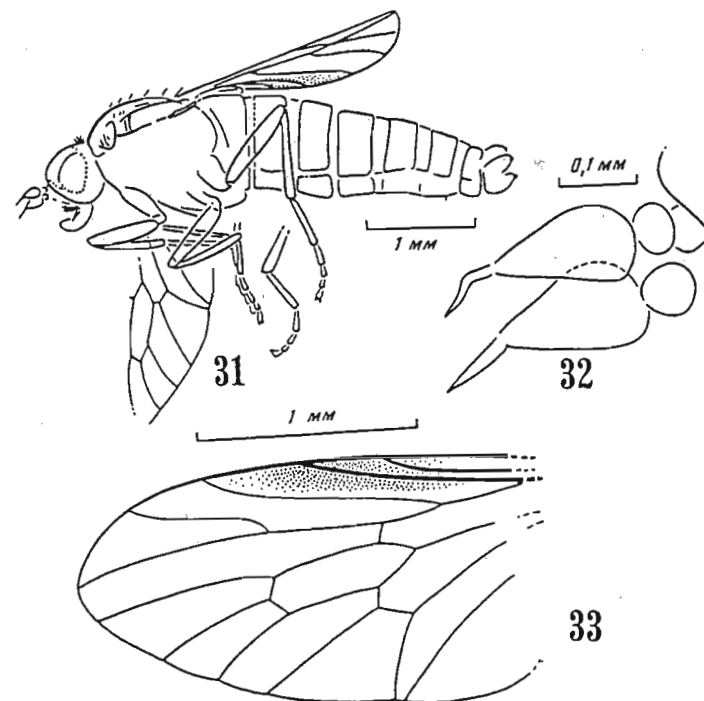
See figs 31–33 [= Kovalev, 1982: fig. 1a,b,c]. Body 4.5 mm (segments of abdomen extended; length of body in living insect was less) and wing 2.8 mm in length. Kovalev (1982 [Russian]; 1982: 88–89 [English translation]) wrote:

Feelers [= palpus] directed horizontally, small, consisting of two segments, covered with hairs, second segments of feelers not widened [on p. 88] ... with rounded tip [on p. 89]. Proboscis shorter than height of head, directed downward and slightly forward, with broad, soft oral disc. ... Arista almost half as long as third segment ... Costal vein strong on anterior margin of wing, thin, but distinct on posterior margin. ... Apical spurs not seen on the tibiae. ... Mesonotum with a few quite short chaetae and hairs; notopleural chaetae longer than the others; humeral callosities with isolated hairs.

Palaeoptiolina is separated from *Rhagionempis* by having vein R_5 longer than the distance between base of R_4 and r-m crossvein and from *Probolbomyia* and *Ussatchovia* by having 4 (not 3) M veins.

Genus *Probolbomyia* Ussatchev, 1968, *Entomol. Obozr.*, 47: 620. Type species: *Probolbomyia modesta* Ussatchev, 1968, by original designation. *modesta* Ussatchev, 1968: 620. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 34 [= Ussatchev, 1968: fig. 3]. Body c.4.5 mm and wing c.3.0 mm in length. "Anal lobe of wing well developed, with protruding margin. Alula developed." Kovalev (1982 [Russian]; 1982: 93 [English translation]) wrote:



Figs 31–33. — *Palaeoptiolina scobloi* Kovalev, ♂ (Rhagionempididae). 31, body; 32, antennae; 33, wing. From Kovalev (1982).

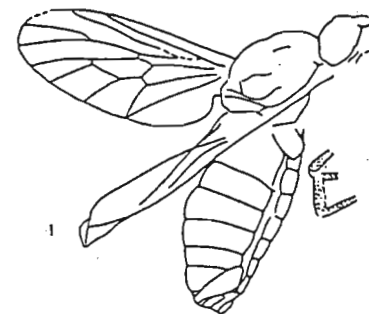
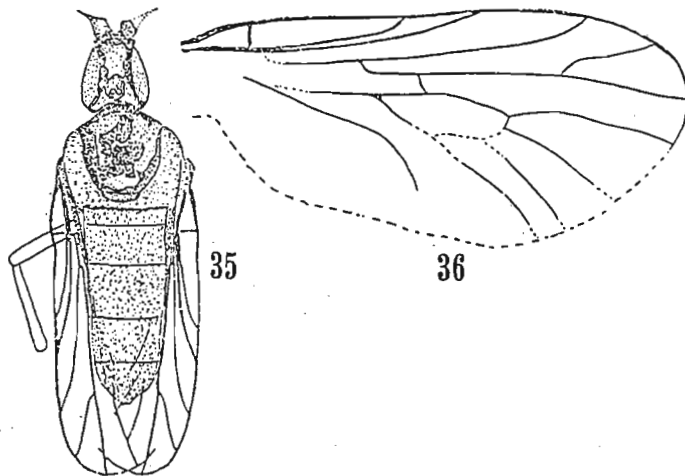


Fig. 34. — *Probolbomyia modesta* Ussatchev, ♀ (Rhagionempididae). From Ussatchev (1968).

The description of *Probolbomyia* is based on a single specimen, from the Malmian of the Karatau region. In this specimen, the holotype of *P. modesta* Ussatchev, the antennae are not preserved. In the material from the Karatau region I found a specimen of *Probolbomyia*, that is probably conspecific with *P. modesta*. The structure of its antennae is the same as in *Ussatchovia*, which may be an argument in favour of combining the two genera. But such action would inevitably lead to difficulties with the interrelationships of the Jurassic faunas of Siberia and Central Asia, and therefore I hesitate to unite them. There is no solid basis for combining them. In the single specimen from which the genus *Ussatchovia* was described, the middle part of the wing is poorly preserved, and it is possible that M_4 is not included in the posterior margin of the discoidal cell, as in *Probolbomyia*, but leaves at the point of contact of the cell with m-cu. In that case, *Probolbomyia* and *Ussatchovia* cannot be said to be congeneric. Therefore, I still prefer to regard them as separate genera.

The wing venation of *Probolbomyia* would be identical with that of *Bolbomyia* of Rhagionidae, if (1) vein R_5 is longer than (2) distance between base of R_4 and m-cu crossvein. In *Bolbomyia*, antennal segment 3 is ovate and with a thick 2–3 jointed prolongation in which each joint is shorter than segment 3 (= flagellomere 1). The (1) above is distinctly less than twice as long as the (2) in *Probolbomyia* but roughly twice as long as the (2) in *Bolbomyia*.

Genus *Rhagionempis* Rohdendorf, 1938, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, 7(3): 34. Type species: *Rhagionempis tabanicornis* Rohdendorf, 1938, by original designation.
tabanicornis Rohdendorf, 1938: 35. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].



Figs 35–36. — *Rhagionempis tabanicornis* Rohdendorf, ♀ (Rhagionempididae). 35, body; 36, wing. From Rohdendorf (1938).

See figs 35–36 [= Rohdendorf, 1938: figs 4–5]. Body 3.75 mm and wing 3.5 mm in length. Anal cell closed, but perhaps sometimes narrowly open as in *Palaeoptiolina*. Probably vein M_4 arising from 2nd basal cell as in *Palaeoptiolina*. Kovalev (1982; 1982: 89 & 96 [English translation]) wrote:

In the new collections I have found four impressions of *Rhagionempis*, that are well preserved ...; at least the first of these is conspecific with *R. [tabanicornis]*. ... the pronothous position of the head in the holotype of *R. [tabanicornis]* mentioned in the original description is a result of deformation. The apparent angularity of the third segment of the antennae has been caused by chipping off of the organic layer. ... Head round, slightly flattened posteriorly, as in *Palaeoptiolina*. Third segment of antennae is rounded-triangular, as in the genus being compared. Costal vein runs round entire wing, becoming thinner beyond its tip. R_5 shorter than the trunk of the fork R_{4+5} . Anal cell closed on wing margin. ... Among the Jurassic rhagionids with four branches of M, the closest to *Palaeoptiolina* is *Rhagionempis*, in which R_4 also bends towards the anterior margin of the wing. *Palaeoptiolina* differs from this genus in its longer fork of R_4 and R_5 ; the last vein in *Palaeoptiolina* is longer than the trunk of the fork, but in *Rhagionempis* it is shorter.

Genus *Shevioptera* Kalugina, 1989, *Paleontol. Zh.*, 1989(1): 73. Type species: *Shevioptera sinitsae* Kalugina, 1989, by original designation.
sinitsae Kalugina, 1989: 73. Palaeartic: Russia (Siberia) (Upper Jurassic/Lower Cretaceous) [Compression or impression].

See figs 37–46 [= Kalugina, 1989: fig. 4a–j]. Abdomen 4.5 mm and wing 4.2 mm in length. [Head and thorax unknown.] Kalugina (1989) placed *Shevioptera* originally in Eoptychopteridae (Nematocera). *Shevioptera* is similar to *Proptychoptera* and *Proptychopterina* in having vein M_4 arising from discal cell but is at once distinguished from them in the following points:

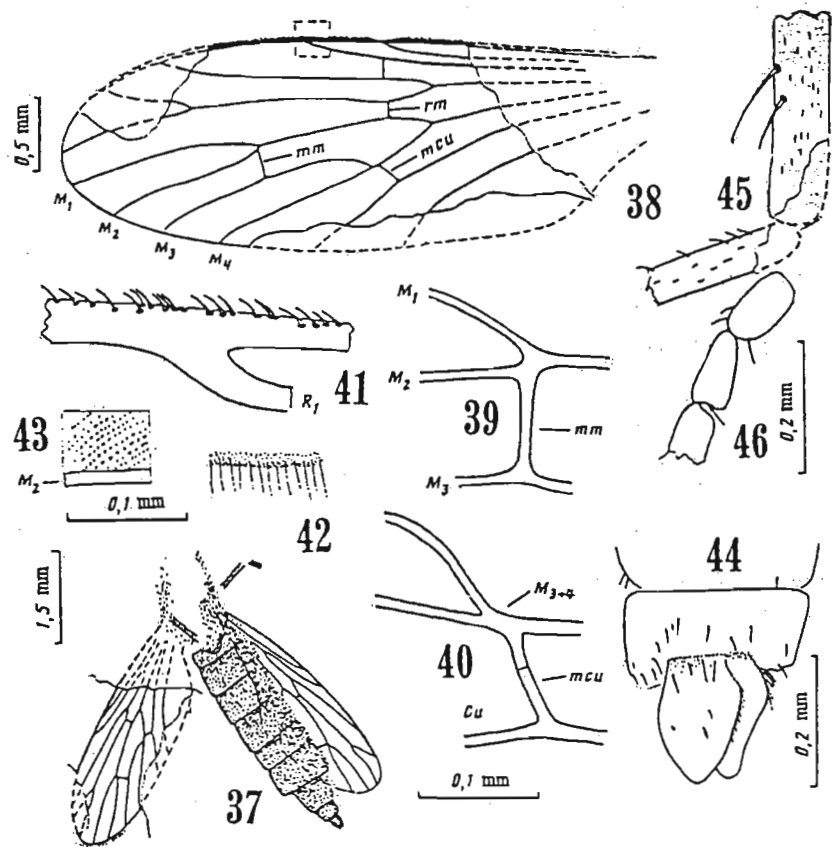
mouth of subcostal cell much shorter than wing margin between R_1 and R_4 ; 2nd submarginal cell short and vein R_5 distinctly shorter than trunk of R_4+R_5 ; vein M_1 not shorter than discal cell; base of vein M_4 situated very near m-cu crossvein; r-r crossvein situated opposite r-m crossvein. No fundamental difference is found in female cercus structure between *Eoptychopterina daiensis* Kalugina and *Shevioptera sinitsae* Kalugina.

Shevioptera differs markedly from the members of Rhagionempididae in the following respects: r-r crossvein present and anal cell apparently divergent apically.

However, Lukasevitch (1994) wrote:

After a survey of both described [Kovalev, 1982] and undescribed Rhagionidae from the Upper Jurassic-Lower Cretaceous of Transbaykalia, it can be concluded that *Shevioptera sinitsae* Kalugina, 1989 from the same beds does not belong to Eoptychopteridae (not included in the key below). It is probably Rhagionidae, close to *Rhagionempis* Rohdendorf and *Ussatchovia* Kovalev in venation (short fork of R_{4+5} , 4 medial branches, m-cu meeting M_{3+4} , symmetrical first fork of M, closed anal cell). Contrary to fig. 4 in Kalugina (1989), R_2 [= crossvein r-r] is absent and cerci appear to be two-segmented – both characteristic of Rhagionidae.

If r-r crossvein is absent and anal cell is closed, *Shevioptera* would belong in or near either Rhagionidae (when cercus is 2-segmented) or Rhagionempididae (when 1-segmented). *Shevioptera* is here placed in Rhagionempididae quite provisionally but is excluded from the key to genera.



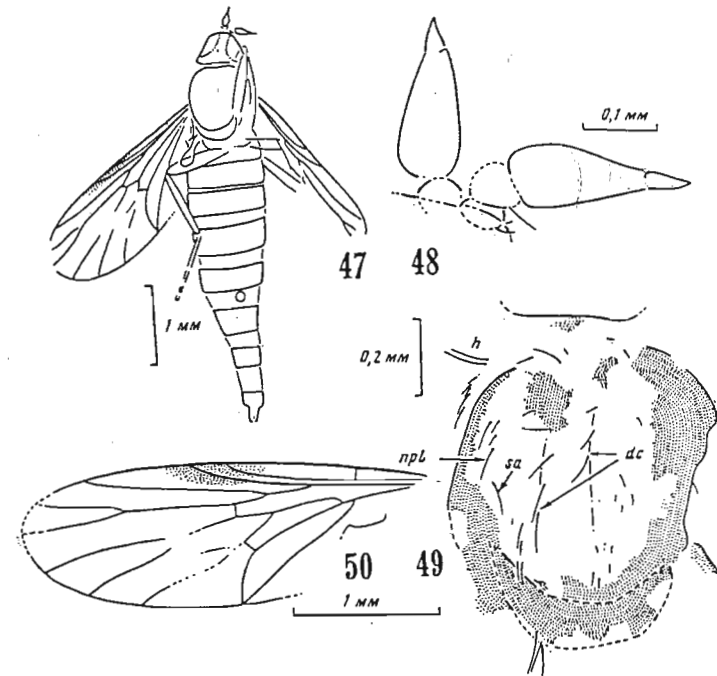
Figs 37-46. — *Shevoptera sinitsae* Kalugina, ♀ (? Rhagionempididae). 37, abdomen, dorsal view; 38, wing; 39, crossvein m-m; 40, crossvein m-cu; 41, spinules on costal vein near R_1 ; 42, bristles on posterior margin of wing; 43, microtrichia near vein M_2 ; 44, tip of abdomen including ♀ cerci; 45, part of femur and tibia; 46, part of tarsus. From Kalugina (1989).

Genus *Ussatchovia* Kovalev, 1982, *Paleontol. Zh.*, 1982(3): 91. Type species: *Ussatchovia jurassica* Kovalev, 1982, by original designation. *jurassica* Kovalev, 1982: 92. Palaeartic: Russia (Siberia) (Middle Jurassic) [Compression or impression].

See figs 47-50 [= Kovalev, 1982: fig. 1d-g]. Body 5.0 mm (abdominal segment greatly extended; length of living insect was less) and wing 2.7 mm in length. Kovalev (1982 [Russian]; 1982: 90 & 93 [English translation]) wrote:

[Head and its appendages] have the same structure as those in *Palaeoptolina*; arista shorter than third segment. Thorax with few chaetae, humeral, dorsocentral, supra-alar, and notopleural groups are distinguishable. Scutum short, with chaetae on posterior margin. ...

Costal segment between R_1 and R_{2+3} much longer than that between Sc and R_1 R_4 and R_5 diverge at an acute angle almost symmetrically relative to their trunk. ... M_4 for some distance evidently fuses with posterior margin of discoidal cell (as in *Probolbomyia* Ussatchev) or leaves it where it joins cell m-cu; at any rate, the segment of M_4 between the cell and m-cu that is found, for example, in *Palaeoptolina*, is not apparent here. ... Alula developed but small. ... Ovipositor begins with segment VIII, and is separated from VII by a connecting membrane that is longer than between the other pairs of segment. Cerci elongated (division into two segments not apparent), are covered with sparse hairs.



Figs 47-50. — *Ussatchovia jurassica* Kovalev, ♀ (Rhagionempididae). 47, body, dorsal view; 48, antennae; 49, mesonotum and scutellum; 50, wing. dc, dorsocentral bristle; h, humeral; npl, notopleural; sa, supra-alar. From Kovalev (1982).

Ussatchovia has no vein M_3 , but *Palaeoptolina* and *Rhagionempis* each has it. For distinction between *Ussatchovia* and *Probolbomyia*, see note under *Probolbomyia* (p. 122).

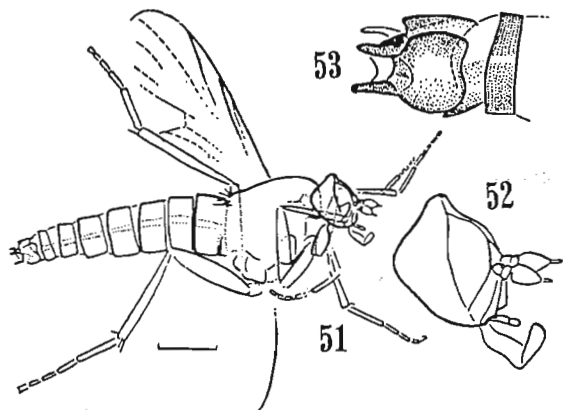
Gen. et sp. 1 by Kovalev, 1986, *Trudy Sovmest. Sov.-Mongol. Paleontol. Eksped.*, 28: 145. Palaeartic: Mongolia (Lower Cretaceous) [Compression or impression].

See figs 51-53 [= Kovalev, 1986: fig. 116a,b,c]. Detail of wing venation is unknown.

Body 5.9 mm and wing 3.8 mm in length.

(1) Male terminalia in fig. 53 probably represent tergum 9 and surstyli.

(2) Spines on apex of mid and hind tibiae are probably not spurs but bristles. Antennal flagellum rounded triangular and with short style probably pointed at apex. Palpus rounded apically and 2-segmented. Proboscis well developed. Mouth of marginal cell wide. Anal cell closed far before wing margin. It is roughly interpreted from fig. 51 that discal cell has 3 veins (vein M_3 or M_4 is absent).



Figs 51–53. — Gen. et sp. 1 by Kovalev, ♂ (Rhagionempididae). 51, body; 52, head; 53, ♂ genitalia (tergum 9 and surstyli). From Kovalev (1986).

If (1) and (2) above are correct, the identity of this genus would not be Rhagionidae (of which *Ptiolina* and *Ptiolinites* may resemble Gen. et sp. 1) but Rhagionempididae (= Apsilocephalidae).

KEY 5: MESOZOIC GENERA OF RHAGIONEMPIDIDAE BASED ON WING CHARACTERS.

- 1 Four M-veins present; mouth of marginal cell nearly as long as or longer than that of 1st submarginal cell 2
- Three M-veins present (probably this is so in Gen. et sp. 1); mouth of marginal cell much shorter than that of 1st submarginal cell (probably this is not so in Gen. et sp. 1) 3
- 2 Vein R_5 distinctly longer than distance between base of R_4 and m-cu crossvein; (figs 31–33) *Palaeoptiolina*
- Vein R_5 shorter than distance between base of R_4 and m-cu crossvein; (figs 35–36) *Rhagionempis*
- 3 Anal cell closed at wing margin 4
- Anal cell closed far before wing margin; (figs 51–53) Gen. et sp. 1 of Kovalev (1986)
- 4 Distance between base of M_4 and m-cu crossvein longer than basal section of discal cell; (fig. 34) *Probolbomyia*
- Distance between base of M_4 and m-cu crossvein shorter than basal section of discal cell (or possibly vein M_4 arising from 2nd basal cell) (figs 47–50) *Ussatchovia*

FAMILY RHAGIONIDAE

The genera below have the following common characters in the wing:

Vein R_5 ends at, near or far below wing apex; wing margin between R_1 and R_4 much longer than mouth of subcostal cell and than mouth of 2nd submarginal cell; mouth of marginal cell distinctly shorter than that of 1st submarginal cell (except *Kubekovia*); 4th (or 3rd + 4th) posterior cell long and wide open; vein Cu_1 at least $1/2$ as long as posterior section of 2nd posterior cell; alula present.

The antennal flagellum of Rhagionidae is various in shape: subulate and multi-segmented; with widened base (= flagellomere 1) bulbous (sometimes longer than wide) and having a segmented or unsegmented style or arista; etc. (see Nagatomi, 1981: 399–400; 1982: figs 4–25).

The Mesozoic extinct Rhagionidae are similar to Protobranchyridae, Rhagionempididae and the genus *Ija* but are separated from them as shown in key 4 (p. 100) (couplets 13, 14 & 18).

The significant difference between Rhagionidae and Pelecorhynchidae is found in larval stage only (see Teskey, 1970; Woodley, 1989), but the genera (*Glutops*, *Pelecorhynchus* and *Pseudoerinna*) of Pelecorhynchidae may be separated from those of Rhagionidae as shown in key 1 (p. 98) (especially couplets 5 & 27).

The extinct genus *Kubekovia* may be distinguished from *Glutops* and *Pseudoerinna* (living genera of Pelecorhynchidae) by having the mouth of marginal cell longer than (not nearly as long as) that of 1st submarginal cell, and 2nd submarginal cell long and with base situated opposite far before (not beyond) apex of discal cell. *Kubekovia* belongs in either Rhagionidae or Pelecorhynchidae but is placed here tentatively in the former which is larger in the number of genera than the latter.

Genus *Jurabrachyceron* Kovalev, 1981, *Paleontol. Zh.*, 1981(3): 92. Type species: *Jurabrachyceron abbreviatum* Kovalev, 1981, by original designation.

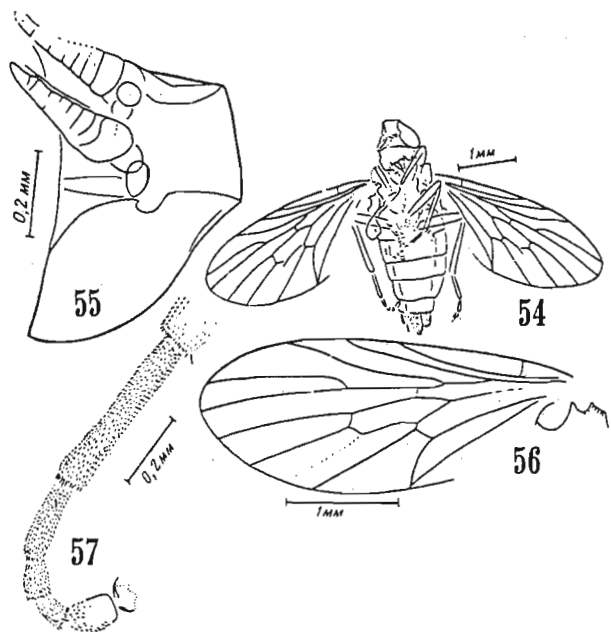
abbreviatum Kovalev, 1981: 93. Palaeartic: Russia (Siberia) (Middle/Upper Jurassic) [Compression or impression].

See figs 54–57 [= Kovalev, 1981: fig. 2c–f].

Body 3.7 mm and wing 3.5 mm in length. Antennal flagellum wider than scape or pedicel, 8-segmented, and pointed at apex; alula well developed; mouth of marginal cell much shorter than that of 1st submarginal cell; vein M_3 absent or vestigial; anal cell closed; empodium probably pulvilli or pad-like. Kovalev (1981) wrote, “ R_5 reaches wing margin at point of its apex”, but it may be also interpreted that R_5 ends below wing apex. It is interpreted that vein Cu_1 is about $1/2$ (not distinctly less than $1/2$) as long as posterior section of 2nd basal cell.

Jurabrachyceron would fall in couplet 11 of key 1, if vein R_5 ends at wing apex, but is easily separated from *Bolbomyia*, *Spania* and *Spaniopsis* where antennal flagellum is not 8-segmented. It would fall in upper branch of couplet 23, if vein R_5 ends far below wing apex, but is easily separated from *Dialysis* (Coenomyiidae) where antennal flagellum has an unsegmented arista. It would fall in lower branch of couplet 30, if the absence of vein M_3 is disregarded, but may be separated from the living

genera of Coenomyiidae by having vein R_{2+3} ending more distantly from apex of R_1 . It is separated from Pelecorhynchidae (*Glutops* and *Pseudoerinna*) where mouth of marginal cell is nearly as long as that of 1st submarginal cell.



Figs 54–57. — *Jurabrachyceron abbreviatum* Kovalev, ♀ (Rhagionidae). 54, body, ventral view; 55, frons and antennae; 56, wing; 57, hind tarsus and apex of tibia. From Kovalev (1981).

Genus *Kubekovia* Kovalev in Kalugina & Kovalev, 1985, *Dipterous insects of Jurassic Siberia*, Paleontological Institute, Akademia Nauk, Moscow, p. 185. Type species: *Kubekovia accessoria* Kovalev, 1985, by original designation.

accessoria Kovalev in Kalugina & Kovalev, 1985: 185. Palaeartic: Russia (Siberia) (Middle Jurassic) [Compression or impression].

Only wing is known. Wing length 4.2 mm. Postero-proximal part of wing is unknown. See fig. 58 [= Kalugina & Kovalev, 1985: fig. 120]. First posterior cell would have a crossvein, if this crossvein is normal.

Kubekovia would fall in lower branch of couplet 27 of key 1, if vein R_5 ends far below wing apex. It is distinguished from *Glutops* and *Pseudoerinna* by having vein Cu_1 longer and 2nd submarginal cell longer and with base opposite distinctly before apex of discal cell. It may easily be separated from the living genera of Rhagionidae (except *Bolbomyia*) by

having (1) mouth of marginal cell longer than (2) that of 1st submarginal cell. In *Bolbomyia*, (1) above is nearly as long as (2), but vein R_5 ends at (not far below) wing apex and wing with 4 (not 5) posterior cells.

It would fall in lower branch of couplet 19 of key 1, if vein R_5 ends at wing apex. However, it may easily be separated from *Ptiolina* and *Spania* by having mouth of marginal cell longer than that of 1st submarginal cell.

It is difficult to determine whether *Kubekovia* belongs in Pelecorhynchidae or Rhagionidae, because some species of *Glutops* (Pelecorhynchidae) may have vein Cu_1 relatively long, but *Kubekovia* is here placed tentatively in Rhagionidae.

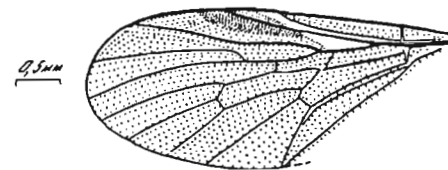


Fig. 58. — *Kubekovia accessoria* Kovalev (Rhagionidae), wing. From Kalugina & Kovalev (1985).

Genus *Palaeobrachyceron* Kovalev, 1981, *Paleontol. Zh.*, 1981(3): 87.

Type species: *Palaeobrachyceron handlirschi* Kovalev, 1981, by original designation.

handlirschi Kovalev, 1981: 89 (body 4.7 mm and wing 3.2 mm in length;

hennigi Kovalev, 1981: 89 (body 3.7 mm and wing 3.2 mm);

nagatomii Kovalev, 1981: 91 (wing 2.7 mm);

rohdendorfi Kovalev, 1981: 91 (body 5.1 mm and wing 3.7 mm);

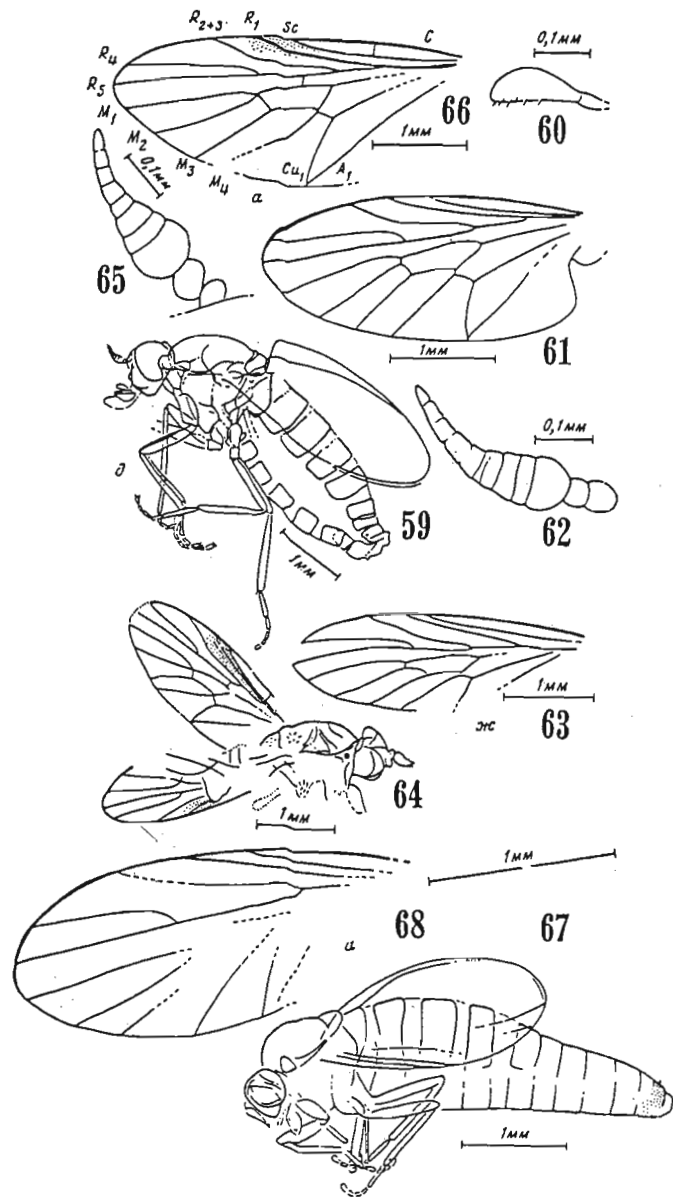
steyskali Kovalev, 1981: 92 (body 4.2 mm and wing 2.3 mm). Palaeartic:

Russia (Siberia) (Middle/Upper Jurassic) [Compression or impression].

See figs 59–68 [= Kovalev, 1981: figs 1a–h, 2a,b].

Antennal flagellum wider than scape or pedicel, 8–9 segmented, and pointed at apex (visible in *rohdendorfi* and *hennigi*); palpal segment 2 widened (visible in *handlirschi*); alula well developed (visible in *handlirschi*) and wing wide; vein R_5 ends at wing apex; vein R_{2+3} ends far beyond apex of R_1 but mouth of marginal cell much shorter than that of 1st submarginal cell; 4th posterior cell wide open; anal cell closed; vein Cu_1 at least $1/2$ as long as posterior section of discal cell; distance between h crossvein and base of R_s may be shorter than basal section of R_s (visible in *rohdendorfi* and *handlirschi*).

The wing venation falls in lower branch of couplet 19 of key 1, (p. 99) (i.e., *Ptiolina* and *Spania*) where antennal flagellum has an unsegmented style by which the latter two are easily distinguished from *Palaeobrachyceron*. *Palaeobrachyceron* is easily separated from the Vermilionidae and the Xylophagoidea by having vein Cu_1 at least $1/2$ as long as posterior section of 2nd basal cell. It would be at once distinguished from *Palaeostratiomyia* Rohdendorf, if anal cell of the latter is wide open.

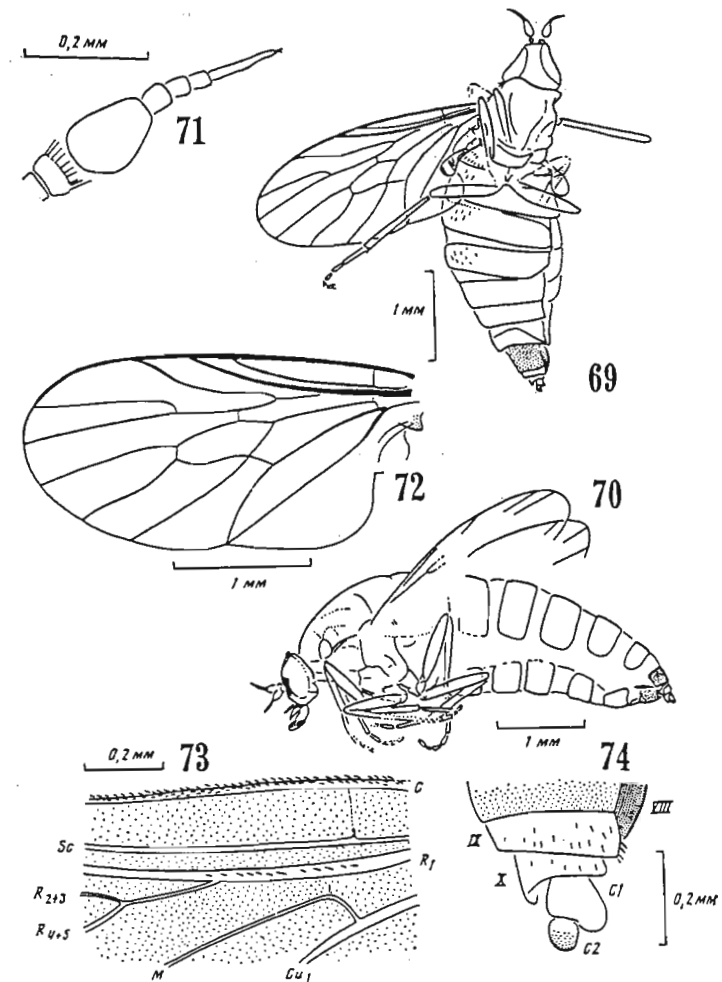


Figs 59–68. — *Palaeobrachyceron* spp. (Rhagionidae). 59–61, *handlirschi* Kovalev, ♂ (59, body; 60, palpus; 61, wing). 62–63, *hennigi* Kovalev (62, antenna; 63, wing). 64, *nagatomii* Kovalev. 65–66, *rohdendorfi* Kovalev (65, antenna; 66, wing). 67–68, *steyskali* Kovalev (67, body; 68, antenna). From Kovalev (1981).

Genus *Palaeobolbomyia* Kovalev, 1982, *Paleontol. Zh.*, 1982(3): 94. Type species: *Palaeobolbomyia sibirica* Kovalev, 1982, by original designation.

sibirica Kovalev, 1982: 95. Palaearctic: Russia (Siberia) (Middle Jurassic) [Compression or impression].

See figs 69–74 [= Kovalev, 1982: fig. 2a–f]. Body 4.0–4.5 mm and wing 2.8–2.9 mm in length. Male unknown.



Figs 69–74. — *Palaeobolbomyia sibirica* Kovalev, ♀ (Rhagionidae). 69–70, body; 71, antenna; 72, wing; 73, part of wing; 74, apex of abdomen. C₁ and C₂, segments 1–2 of cercus. From Kovalev (1982).

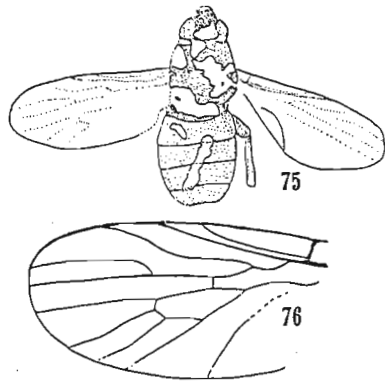
Antennal flagellum with a thick 4-segmented style pointed at apex; flagellomere 1 egg-shaped and longer than wide. Palpus may be pointed at apex. Vein R_5 ends at wing apex; vein R_{2+3} ends far beyond apex of R_1 , but mouth of marginal cell is much shorter than that of 1st submarginal cell; vein M_3 absent; anal cell closed at wing margin; wing wide and alula well developed. Cercus 2-segmented and with segment 1 dilated posterolaterally.

Palaeobolbomyia falls in lower branch of couplet 11 of key 1, that is, *Bolbomyia*, but may differ from the latter in the following respects: last flagellomere pointed at apex; palpus may be pointed at apex; female frons may be narrower than one eye [which is apparently depressed in fig. 68].

Genus *Palaeostratiomyia* Rohdendorf, 1938, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, 7(3): 32. Type species: *Palaeostratiomyia pygmaea* Rohdendorf, 1938, by original designation. *pygmaea* Rohdendorf, 1938: 33. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

Body 2.75 mm and wing 2.5 mm in length. Antenna and proboscis unknown; alula unknown. Judged from figs 75–76 [= Rohdendorf, 1938: figs 2–3]:

vein R_5 ends at wing apex; 2nd submarginal cell long and parallel-sided (except base); vein M_4 arising from discal cell; distance between humeral crossvein and vein R_s shorter than basal section of R_s ; anal cell may possibly be wide open.



Figs 75–76. — *Palaeostratiomyia pygmaea* Rohdendorf, ♀(?) (Rhagionidae). 75, body; 76, wing. From Rohdendorf (1938).

Rohdendorf (1938: 57–58) wrote,

“C am Rande des Flügels nur bis zum Ende der R_{s_3} [= vein R_5] reichend. ... Stirn breit, ca 1 1/2 – mal so breit als das Auge; Gesicht nur etwas vorstehend; ... Abdomen kurz eiförmig, aus 4 (2.–5. Tergite) Segmenten bestehend.”

Palaeostratiomyia would be similar to '*Neorhagio*' (sensu Nagatomi, 1982), if anal cell were wide open, anal lobe were narrow and alula were vestigial. However in the latter, vein R_5 ends far below wing apex, vein

M_4 arises from 2nd basal cell, 2nd submarginal cell divergent apically, and distance between humeral crossvein and vein R_s is longer than basal section of R_s .

It would be similar to *Spania*, if anal cell were closed, anal lobe were wider and alula were well developed. However in the latter, vein M_4 arises from 2nd basal cell.

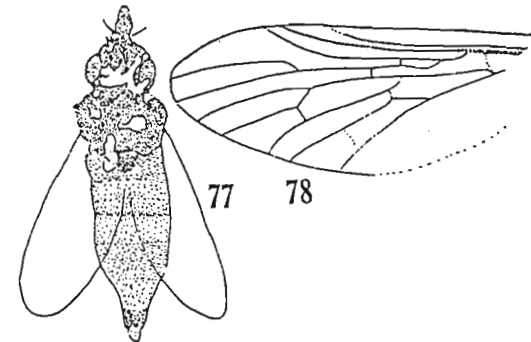
It also differs from *Bolbomyia* by having 5 (not 4) posterior cells.

Genus *Protorhagio* Rohdendorf, 1938, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, 7(3): 37. Type species: *Protorhagio capitatus* Rohdendorf, 1938, by original designation. *capitatus* Rohdendorf, 1938: 38. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

Body 6.5 mm and wing 5.0 mm in length. Legs and postero-proximal part of wing unknown.

Judged from figs 77–78 [= Rohdendorf, 1938: figs 9–10]:

vein R_5 ends below wing apex; vein R_{2+3} is curved upward and ends rather near apex of R_1 ; 4th posterior cell wide open; vein M_4 arising from 2nd basal cell; marginal cell much longer than 1st basal cell; vein Cu_1 much longer than posterior section of 2nd basal cell; there is a crossvein in 1st submarginal cell, but if abnormal in condition, the presence of this vein would have no significance taxonomically.



Figs 77–78. — *Protorhagio capitatus* Rohdendorf, ♀(?) (Rhagionidae). 77, body; 78, wing. From Rohdendorf (1938).

Rohdendorf (1938: 60) wrote,

“C die Flügelspitze übergehend, Ende der C undeutlich. ... R_{s_3} [= vein R_4] vor, R_{s_4} hinter der Flügelspitze mündend. ... Augen klein, Stirn mindestens 2-mal so breit als das Auge. ... Arista dünn und lang, borstenförmig. ... Abdomen ..., in der Basalhälfte breit, am Ende verschmälert.”

Protorhagio is easily separated from (1) Coenomyiidae (*Dialysis*), (2) Pelecorhynchidae (*Glutops* and *Pseudoerinna*) and (3) Athericidae where (1): vein Cu_1 less than 1/2 as long as posterior section of 2nd basal cell and

4th posterior cell closed; (2): mouth of marginal cell nearly as long as that of 1st submarginal cell; (3): marginal cell about as long as 1st basal cell and vein Cu_1 shorter than posterior section of 2nd basal cell.

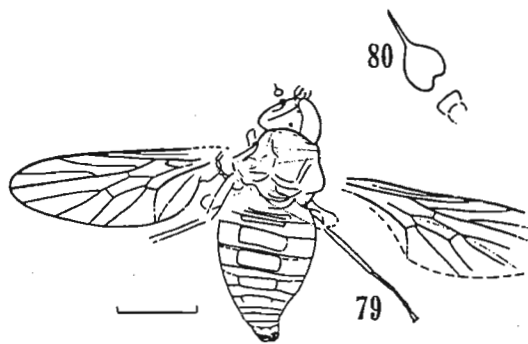
The wing venation of *Protorhagio* may most closely resemble that of *Chrysopilus* and *Symphoromyia* but is distinguished from the latter by having vein Cu_1 much longer than posterior section of 2nd basal cell.

Protorhagio probably belongs to Rhagionidae.

Genus *Ptiolinites* Kovalev, 1986, *Trudy Sovmest. Sov.-Mongol. Paleontol. Eksped.*, 28: 143. Type species: *Ptiolinites cretaceus* Kovalev, 1986, by original designation.

cretaceus Kovalev, 1986: 143. Palaeartic: Mongolia (Lower Cretaceous) [Compression or impression].

See figs 79–80 [= Kovalev, 1986: fig. 115a,b]. Body 3.1 mm and wing 2.4 mm in length. Antennal flagellum is similar in shape to that of *Ptiolina*. *Ptiolinites* would be identical with *Ptiolina*, if the following characters are not significant generically: vein R_{2+3} straight and ending more distantly from apex of R_1 ; vein M_2 arising from vein M_1 . It is necessary to find a sounder generic character for the establishment of *Ptiolinites*.



Figs 79–80. — *Ptiolinites cretaceus* Kovalev, ♂ (Rhagionidae). 79, body and wings; 80, antenna. From Kovalev (1986).

Genus *Rhagiophryne* Rohdendorf, 1964, *Trudy Paleontol. Inst. Akad. Nauk SSSR*, 100: 233. Type species: *Rhagiophryne bianalis* Rohdendorf, 1964, by original designation.

bianalis Rohdendorf, 1964: 234. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

Rhagiophryne and *bianalis* of Rohdendorf (1951: 79, 84; 1962: 337) are nomina nuda (in accordance with Article 13 of The Code).

See fig. 81 [= Rohdendorf, 1962: fig. 1091]. Only wing (whose length is 4.5 mm) is known. Wing is wide and alula is probably present.

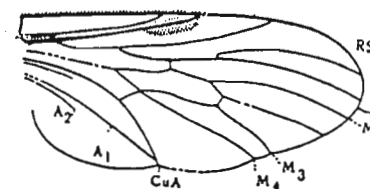


Fig. 81. — *Rhagiophryne bianalis* Rohdendorf (Rhagionidae), wing. From Rohdendorf (1962).

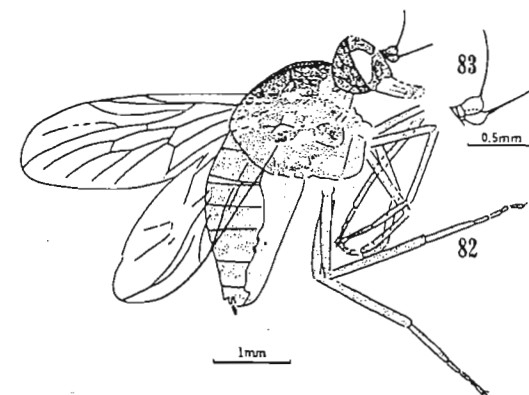
Rohdendorf (1964; 1974: 263 [English translation]) wrote,

“Highly noticeable is the clear short vein located behind A_1 ; it is parallel with it and presumably is A_2 .”

It is deduced that vein R_5 ends far below wing apex.

Rhagiophryne falls in lower branch of couplet 31 of key 1 but is distinguished from *Arthroteles*, *Atherimorpha*, *Rhagio*, *Symphoromyia* and *Ptiolina* by having vein R_{2+3} ending more distantly from apex of R_1 . *Rhagiophryne* is most similar to *Arthroceras* by having distance between humeral crossvein and base of R_s shorter than basal section of R_s , and a distinction between them may be difficult apart from the presence or absence of vein ‘ A_2 ’, but in *Arthroceras* vein Sc is longer and ends far beyond opposite r-m crossvein.

Genus *Scelorhagio* Zhang (J.), Zhang (S.) & Li, 1993, *Acta Palaeontol. Sinica*, 32: 664. Type species: *Scelorhagio mecomastigus* J. Zhang, S. Zhang & Li, 1993, by original designation.
mecomastigus J. Zhang, S. Zhang & Li, 1993: 665. Palaeartic: China (Upper Jurassic) [Compression or impression].



Figs 82–83. — *Scelorhagio mecomastigus* J. Zhang, S. Zhang and Li (Rhagionidae). 82, body; 83, antenna. From Zhang *et al.* (1993).

See figs 82–83 [= Zhang *et al.*, 1993: fig. 3a,b]. Body 4.0 mm and wing 3.4 mm in length. Zhang *et al.* (1993: 670–671) wrote,

“Antennae ... armed with elongate, likely segmented style. ... Both R_4 and R_5 elongate, running close to each other; and curved downward.”

Vein R_5 probably ends far below wing apex. The following remain uncertain: alula present or absent; marginal cell longer than or about as long as 1st basal cell; vein Cu_1 distinctly less than $1/2$ or at least $1/2$ as long as posterior section of 2nd basal cell. The wing venation of *Scelorhagio* has the base of 3rd posterior cell acutely pointed. The antenna and general appearance of *Scelorhagio* most closely resemble those in *Rhagio* and *Chrysopilus* where base of 3rd posterior cell is not pointed but flat and antennal flagellum is unsegmented.

Genus *Zarzia* Zaitzev, 1986, *Entomol. Obozr.*, **65**: 818. Type species: *Zarzia zherichini* Zaitzev, 1986, by original designation. *zherichini* Zaitzev, 1986: 818. Palearctic (Siberia) (Upper Cretaceous) [Amber].

Zarzia is removed to Rhagionidae by Evenhuis (1990, 1994) from Bombyliidae (Phthiriinae).

Body 1.25 mm and wing 1.1 mm in length. Female unknown. Zaitzev (1986; 1987: 153–154 [English translation]) wrote,

“eyes of δ contiguous for long distance, facets variable in size, larger in upper half of eyes than in lower half; antennal bases close together. First and 2nd antennal segments small, almost equal to each other; 3rd segment bulbous with stylus 3.5 times as long as segment itself; stylus retaining segmentation consists of 6 (possibly 7) segments, borders between which poorly visible due to dense cover of short hairs; proboscis short, not protruding beyond margin of oral depression. ... Occiput flat. ... Only short hairs present on legs, bristles absent. ... Costal vein reaching apex of R_5 .”

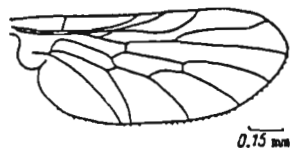


Fig. 84. — *Zarzia zherichini* Zaitzev, δ (Rhagionidae), wing. From Zaitzev (1986).

Judging from fig. 84 [= Zaitzev, 1986: fig. 6], *Zarzia* is similar to (1) *Austroleptis*, (2) *Bolbomyia* and (3) *Spaniopsis* but is easily separated from the latter in which (1) and (2) have anal cell closed and (3) has vein R_{2+3} straight. *Zarzia* is also easily separated from *Austroleptis*, *Bolbomyia* and *Spania* by having antennal flagellum 6 (or 7) segmented.

Gen. et sp. 2 by Kovalev, 1986, *Trudy Sovmest. Sov.-Mongol. Paleontol. Eksped.*, **28**: 146. Palearctic: Mongolia (Lower Cretaceous) [Compression or impression].

Only the wing is known and its postero-proximal part is unknown. Wing length is 3.0 mm. See fig. 85 [= Kovalev, 1986: fig. 117]. It falls in couplet 17 of the key (1) and would belong to Xylophagidae, if the alula were vestigial. However, it is easily separated from *Xylophagus* by having R_{2+3} ending far beyond apex of R_1 and vein Cu_1 at least twice as long as posterior section of discal cell. It would be similar to *Ptiolina* or *Ptiolinites*, if alula is present and antennal flagellum has an unsegmented style. The wing venation of Gen. et sp. 2 is identical with that of *Palaeobrachyceron hennigi* where 3rd posterior cell acutely pointed at base. Gen. et sp. 2 would belong in *Palaeobrachyceron*, if antennal flagellum is 8–9 segmented.

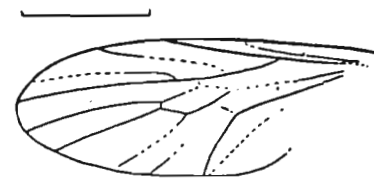


Fig. 85. — Gen. et sp. 2 by Kovalev (Rhagionidae), wing. From Kovalev (1986).

KEY 6: EXTINCT MESOZOIC GENERA OF RHAGIONIDAE

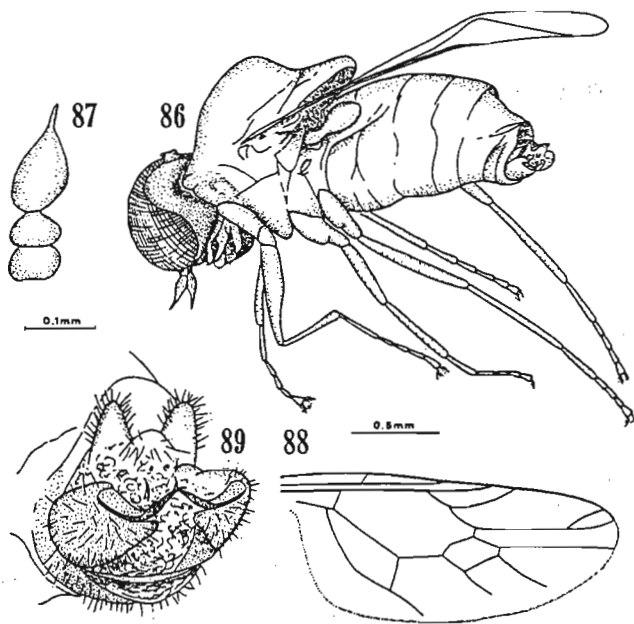
- | | | |
|---|---|------------------------------------|
| 1 | Mouth of marginal cell shorter than that of 1st submarginal cell | 2 |
| — | Mouth of marginal cell longer than that of 1st submarginal cell; (vein Cu_1 over $1/2$ as long as posterior section of 2nd posterior cell; 2nd submarginal cell long and with base ending far before opposite apex of discal cell; 5 posterior cells present; 1st basal cell may possibly have a crossvein); (fig. 58); [only wing known] | <i>Kubekovia</i> |
| 2 | Four posterior cells present | 3 |
| — | Five posterior cells present | 5 |
| 3 | Vein M_4 arising from 2nd basal cell or distance between base of M_3 and m-cu crossvein absent; anal cell closed at wing margin | 4 |
| — | Vein M_4 (if not M_3) arising from discal cell and distance between base of M_3 and m-cu crossvein long; anal cell rather wide open; (antennal flagellomere 1 bulb-shaped with stylus 3.5 times as long as flagellomere 1, 6 or 7 segmented, pointed at apex, and densely covered with short hairs); (fig. 84) | <i>Zarzia</i> |
| 4 | Antennal flagellum with 5 segments of which the last is not shorter than preceding 3 segments; (figs 69–74) | <i>Palaeobolbomyia</i> |
| — | Antennal flagellum with 8–9 segments of which the last is shorter than preceding 3 segments; (figs 54–57) | <i>Jurabrachyceron</i> |
| 5 | Vein R_5 ends at wing apex | 6 |
| — | Vein R_5 ends far below wing apex | 10 |
| 6 | Vein M_4 arising from 2nd basal cell; anal cell closed | 7 |
| — | Vein M_4 arising from discal cell; anal cell may possibly be wide open; (figs 75–76) | <i>Palaeostratiomyia</i> |
| 7 | Third posterior cell acutely pointed at base | 8 |
| — | Third posterior cell not pointed but flat at base | 9 |
| 8 | Antennal flagellum multi-segmented; (figs 62–63) | <i>Palaeobrachyceron (hennigi)</i> |
| — | [Antennal flagellum unknown]; (fig. 85) | Gen. et sp. 2 of Kovalev (1986) |

- 9 Antennal flagellum 8 (or 9) segmented and pointed at apex; (figs 59–61, 64–68) *Palaeobrachyceron*
 — Antennal flagellum with an unsegmented style which is about as long as widened base; (figs 79–80) *Ptiolinities*
- 10 Vein R_{2+3} ends near apex of R_1 (figs 77–78, 82–83); vein A_2 absent; antennal flagellum with a long arista 11
 — Vein R_{2+3} ends far beyond apex of R_1 ; vein A_2 (if so) present; [antennal flagellum unknown]; (fig. 81) *Rhagiophryne*
- 11 Vein Cu_1 much shorter than posterior section of 2nd basal cell; vein Sc ends opposite r-m crossvein; 3rd posterior cell acutely pointed at base; 1st submarginal cell without any crossvein; [it is not necessarily certain whether or not the latter 3 characters above are significant generically]; (figs 82–83) *Scelorhagio*
 — Vein Cu_1 (= distance between apex and discal cell) longer than posterior section of 2nd basal cell; vein Sc ends far beyond opposite r-m crossvein; 3rd posterior cell flat at base; 1st submarginal cell with a crossvein (if this crossvein is normal) before r-m crossvein; (figs 77–78) *Protorhagio*

FAMILY STRATIOMYIDAE

Genus *Cretaceogaster* Teskey, 1971, *Can. Entomol.*, **103**: 1659. Type species: *Cretaceogaster pygmaeus* Teskey, 1971, by original designation.

pygmaeus Teskey, 1971: 1660. Nearctic: Canada (Upper Cretaceous) [Amber].



Figs 86–89. — *Cretaceogaster pygmaeus* Teskey, ♂ (Stratiomyidae: Parhadrestinae). 86, body; 87, antenna; 88, wing; 89, apex of abdomen. From Teskey (1971).

See figs 86–89 [= Teskey, 1971: figs 1–4]. Body 2.2 mm and wing 2.0 mm in length. For detailed description and redescription, see Teskey (1971) and Woodley (1986). Woodley (1986) erected a new subfamily Parhadrestinae for living *Parhadrestia* James, 1975 (with 2 species from Chile) and extinct *Cretaceogaster* and prepared a 'Cladogram showing relationships of the two genera of Parhadrestinae to other Stratiomyoidea'. The wing venation of *Cretaceogaster* is similar to that of *Parhadrestia* but can be separated from the latter by having 2nd submarginal cell short and much shorter than the trunk of R_4+R_5 (see figs 90–91 [= Woodley, 1986: figs 8–9]). The basal cell has a median vein [= M_1] which "is quite faint and not easily seen in the fossil [and] it is little more than a fold in *Parhadrestia*, but is present" (after Woodley, 1986: 387).

The distance between humeral crossvein and base of R_s in Parhadrestinae is about 2–3 times as long as basal section of R_s and is short relative to that of other Stratiomyidae.

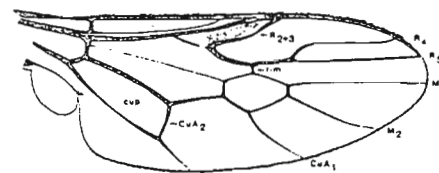


Fig. 90. — *Parhadrestia avata* James (living Stratiomyidae: Parhadrestinae), wing. From Woodley (1986).

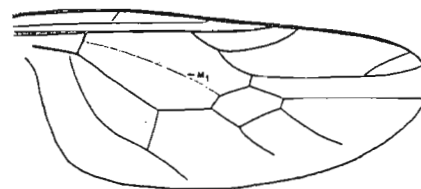


Fig. 91. — *Cretaceogaster pygmaeus* Teskey, wing. From Woodley (1986).

ZHANGSOLVIDAE Fam. n.

Type genus: *Zhangsolva* Nagatomi & Yang.

Genus *Zhangsolva* Nagatomi & Yang, a replacement name for *Archisolva* Zhang (J.), Zhang (S.) and Li, 1993, *Acta Palaeontol. Sinica*, **32**: 662. Type species: *Archisolva cupressa* Zhang (J.), Zhang (S.) & Li, 1993, by original designation.

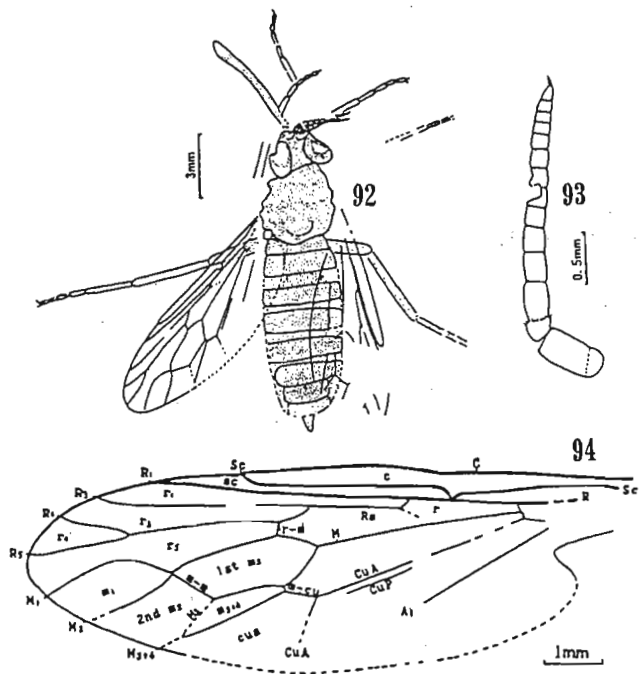
Archisolva Zhang (J.), Zhang (S.) & Li, 1993 is preoccupied by *Archisolva* Enderlein, 1921 (*Mitt. zool. Mus. Berl.*, 10: 187) which is a junior synonym of *Salduba* Walker, 1859 (Stratiomyidae: Pachygastrinae) (after Woodley, 1981).

cupressa Zhang (J.), Zhang (S.) & Li, 1993: 663 (*Archisolva*). Palaearctic: China (Upper Jurassic) [Compression or impression].

See figs 92–94 [= Zhang *et al.*, 1993: figs 1a,b, 2]. Body 14.2 mm and wing 11.0 mm in length.

Zhangsolva falls in lower branch of couplet 14 of the key (1), that is, Xylomyidae. However, it differs very much from the living genera of Xylomyidae by having the following characters:

basal section of vein Rs conspicuously long and with base curved upward (not very short and without base curved upward); antennal flagellum 12-segmented and with a short spine or having 13 segments of which the last is spine-like (not 8-segmented); proboscis (if so) conspicuously long. The costal cell in *Zhangsolva* is concave before Rs and this may possibly represent the crossvein sc-r.



Figs 92–94. — *Zhangsolva* (= *Archisolva*) *cupressa* Zhang (J.), Zhang (S.) & Li, ♀ (*Zhangsolvidae*). 92, body, dorsal view; 93, antenna; 94, wing. From Zhang *et al.* (1993).

Zhang *et al.* (1993: 669) wrote,

“[tibial] spurs invisible; ... Ovipositor short, subtriangular and light-coloured.”

In the living Xylomyidae, tibial spurs are 0 : 2 : 2 (sometimes 0 : 2 : 1 or 0 : 1 : 0) and cercus is 2-segmented. In *Zhangsolva* examined, the tibial spurs and the detail of paired cerci might be overlooked.

In spite of the large differences above the position of *Zhangsolva* is judged to be near Xylomyidae, as thought by Zhang *et al.* (1993), because we have seen no family other than Xylomyidae compatible with *Zhangsolva* throughout Nematocera and orthorrhaphous Brachycera.

The characters of (1) long basal section of Rs and (2) 12 or 13 segmented antennal flagellum, are each apparently in a plesiomorphic state. The 8-segmented antennal flagellum is the ground plan of Brachycera but the very short basal section of Rs might occur independently in each of Stratiomyidae, Xylomyidae and Pantophthalmidae. Let us suppose that *Zhangsolva* belongs to Xylomyidae. Then the character (2) above becomes apomorphic or a reversal to the ancestral form within Xylomyidae. It is more probable on the basis of the character (1) above that *Zhangsolva* represents a stem group of Xylomyidae or that of Stratiomyoidea.

GENERA UNPLACED TO PROPER FAMILY

The position of 8 genera below is uncertain. Evenhuis (1994) placed them as follows: *Batgana* and *Shulmas*, unplaced Tabanoidea; *Ija*, *Mesorhagiophryne*, *Mesostratiomyia*, *Mongolomyia* and *Stratiomyopsis*, Rhagionidae; *Mesomphrale*, Protomphralidae.

Batgana (whose wing venation is unknown) may belong in or near Stratiomyidae.

Ija (whose wing is known in basal part only) is Xylophagoidea or belongs to Pelecorhynchidae of Tabanoidea.

Mesorhagiophryne (where antenna is unknown, and in the type species [*robusta*] m-cu crossvein arises from vein R₂) probably belongs in or near Rhagionidae.

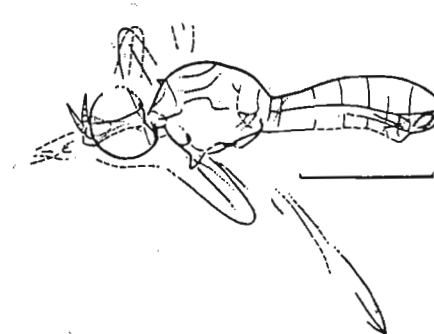


Fig. 95. — *Batgana minor* Kovalev (probably near Stratiomyidae). From Kovalev (1986).

Mesostratiomyia (where apical part of wing is unknown, vein Sc is short and mouth of subcostal cell is markedly long) probably belongs in or near Rhagionidae.

Mesomphrale and *Stratiomyopsis* (where wing venation of each is so peculiar) both belong to the Brachycera other than Empidoidea + Cyclorrhapha.

Mongolomyia (whose wing venation is not clear) represents Xylomyidae, a certain family of Xylophagoidea or a Rhagionidae or Pelecorhynchidae.

Shulmas (of which only the antenna can be clearly seen) belongs in Stratiomyoidea, Xylophagoidea or Tabanoidea but is not a representative of Rachiceridae, Xylophagidae (s. str.) and Athericidae.

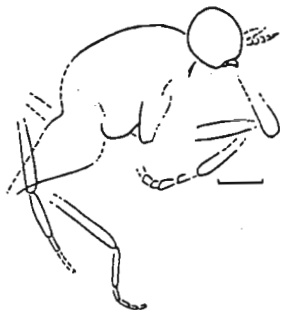


Fig. 96. — *Shulmas globiceps* Kovalev (Stratiomyoidea, Xylophagoidea or Tabanoidea). From Kovalev (1986).

Genus *Batgana* Kovalev, 1986, *Trudy Sovmest. Sov.-Mongol. Paleontol. Eksped.*, 28: 146. Type species: *Batgana minor* Kovalev, 1986, by original designation.

minor Kovalev, 1986: 148. Palaeartic: Mongolia (Lower Cretaceous) [Compression or impression].

Body 2.7 mm in length. Judging from fig. 95 [= Kovalev, 1986: fig. 118], *Batgana minor* (♀) has the following characters:

antennal flagellum multi-segmented and with apex pointed; abdomen widened near posterior end; a lateral process is present probably on mesonotum behind humeral callus; [wing venation unknown].

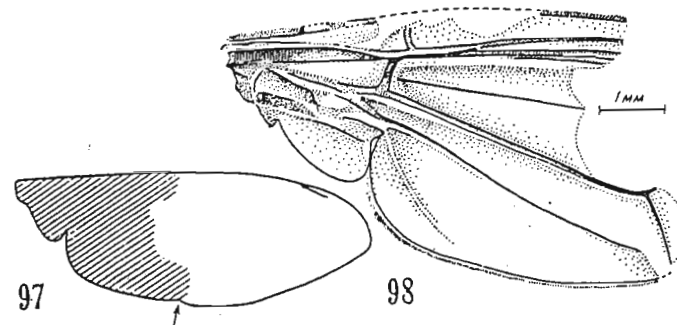
Of the Stratiomyoidea, Xylophagoidea and Tabanoidea, *Batgana* most closely resembles Stratiomyidae in appearance.

Genus *Ija* Kovalev, 1981, *Paleontol. Zh.*, 1981(3): 93. Type species: *Ija problematica* Kovalev, 1981, by original designation.

problematica Kovalev, 1981: 95. Palaeartic: Russia (Siberia) (Middle Jurassic) [Compression or impression].

Only basal part of wing is known. See figs 97–98 (= Kovalev, 1981: 2g,h). Kovalev (1981 [Russian]; 1981: 94–95 [English translation]) wrote:

“alula present, ... Rs long, beginning decidedly proximal to base of discoidal cell. ... Apical segment of Cu_1 short, ... Anal cell with narrow opening. A_1 disappears before reaching margin of wing. ... Among fossil and Recent rhagionids and closely related families, I know of no other forms with A_1 disappearing before reaching margin. This character formed the basis for separating *Ija* as a distinct genus. ... Length of impression to costal vein 6.2 mm; wing length thus apparently 13–14 mm (by analogy with *Rhagio*).”



Figs 97–98. — *Ija problematica* Kovalev (Xylophagoidea or Tabanoidea), wing. From Kovalev (1981).

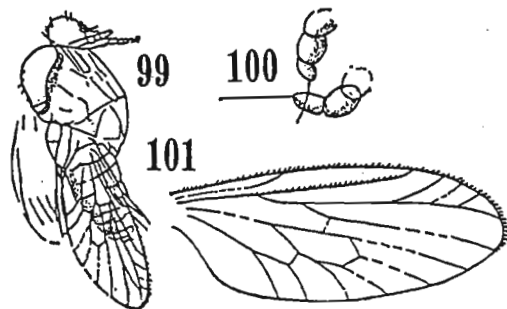
Ija falls in upper branch of key 3. The alula is well developed, so it is not Vermileonidae. If basal section of Rs is long, it would be neither Xylomyidae (apart from Zhangsolvidae placed near Xylomyidae) nor Pantophthalmidae. Thus it certainly represents Xylophagoidea or Pelecorhynchidae of Tabanoidea.

Genus *Mesomphrale* Hong & Wang, 1990, *The stratigraphy and palaeontology of Laiyang Basin, Shandong Province*, (Shandong Bureau of Geology and Mineral Resources, China), p. 156. Type species: *Mesomphrale asiaticum* Hong & Wang, 1990, by original designation.

asiaticum Hong & Wang, 1990: 156. Palaeartic: China (Upper Jurassic) [Compression or impression].

See figs 99–101 [= Hong & Wang, 1990: figs 160–162].

Body 4 mm and wing 3.5 mm in length. Vein Sc short and mouth of subcostal cell conspicuously long; vein R_{2+3} four (or three [if one vein is false]) branched and each branch is short; vein R_{4+5} unbranched and ending far below wing apex; 4th posterior cell markedly divergent apically; vein M_4 arising from discal cell; vein A_1 short and arising beyond middle of 2nd basal cell; [presence or absence of alula unknown]. Antennal scape, pedicel and flagellum each elliptical and with a terminal thin arista which is roughly as long as preceding 2 segments. Each segment of fore and mid tarsomeres is short.



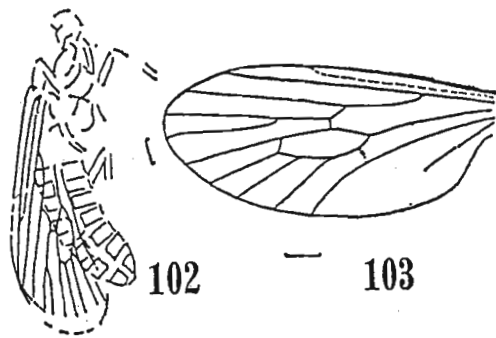
Figs 99–101. — *Mesomphrale asiaticum* Hong & Wang (Brachycera other than Empidoidea + Cyclorrhapha). 99, body; 100, antennae; 101, wing. From Hong & Wang (1990).

Mesomphrale is astonishingly curious in having the characters shown in italics and so cannot be placed in any known family and superfamily, although it certainly belongs to the Brachycera other than Empidoidea + Cyclorrhapha. A new family should be erected for this genus, when more material is available and the peculiarities are confirmed more precisely.

Genus *Mesorhagiophryne* Hong & Wang, 1990, *The stratigraphy and palaeontology of Laiyang Basin, Shandong Province*, (Shandong Bureau of Geology and Mineral Resources, China), p. 152. Type species: *Mesorhagiophryne robusta* Hong & Wang, 1990, by original designation.

incerta Hong & Wang, 1990: 153. Palaeartic: China (Upper Jurassic) [Compression or impression].

See figs 102–103 [= Hong & Wang, 1990: figs 153–154].



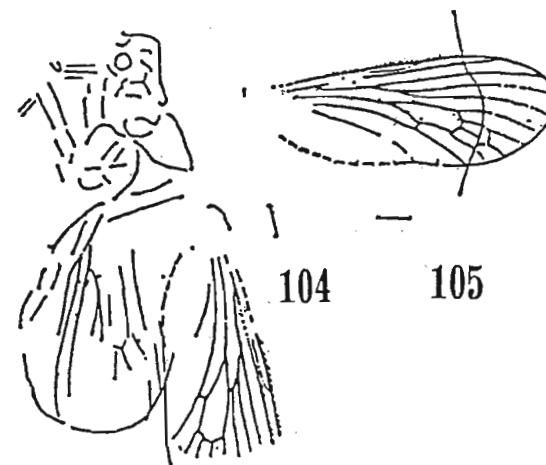
Figs 102–103. — *Mesorhagiophryne incerta* Hong & Wang (probably in or near Rhagionidae). 102, body; 103, wing. From Hong & Wang (1990).

Body 11 mm and wing 10 mm in length. [Head, thorax, legs, apical portion of vein A_1 and presence or absence of alula unclear]. Vein R_4 ending at wing apex and R_5 far below wing apex; vein M_4 arising from discal cell; 4th posterior cell divergent apically; mouth of marginal cell about as long as that of 1st submarginal cell; mouth of 2nd submarginal cell not longer than that of 1st submarginal cell; mouth of subcostal cell probably not shorter than wing margin between R_1 and R_4 ; m-cu crossvein arising from trunk of veins R_4+R_5 .

robusta Hong & Wang, 1990: 152. Palaeartic: China (Upper Jurassic) [Compression or impression].

See figs 104–105 [= Hong & Wang, 1990: figs 151–152]. Body 13 mm and wing 10 mm in length.

[Body, apical part of wing, vein A_1 , presence or absence of alula unclear.] *M. robusta* is apparently similar to *incerta* in wing venation but differs greatly from the latter by m-cu crossvein arising from vein R_5 , and trunk of veins R_4+R_5 short or 2nd submarginal cell markedly long.



Figs 104–105. — *Mesorhagiophryne robusta* Hong & Wang (probably in or near Rhagionidae). 104, body; 105, wing. From Hong & Wang (1990).

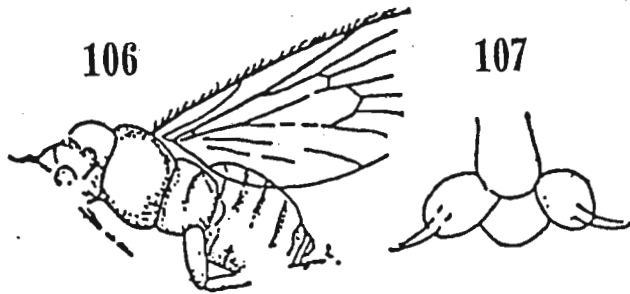
Apart from the situation of m-cu crossvein arising from vein R_5 in *robusta* (the type species), *Mesorhagiophryne* may fall in lower branch of couplet 27 of the key (1), that is, Pelecorhynchidae (*Glutops* and *Pseudoerinna*) but may be distinguished from the latter where the mouth of the subcostal cell is much shorter than wing margin between R_1 and R_4 and the trunk of veins R_4+R_5 longer than vein R_4 or R_5 . *Mesorhagiophryne* is here unplaced to a proper family, although it probably belongs in or near Rhagionidae.

Genus *Mesostratiomyia* Hong & Wang, 1990, *The stratigraphy and palaeontology of Laiyang Basin, Shandong Province*, (Shandong Bureau of Geology and Mineral Resources, China), p. 155. Type species: *Mesostratiomyia laiyangensis* Hong & Wang, 1990, by original designation.

laiyangensis Hong & Wang, 1990: 155. Palaeartic: China (Upper Jurassic) [Compression or impression].

See figs 106–107 [= Hong & Wang, 1990: figs 158–159].

Body 2.2 mm and wing 2.2 mm in length. [Details of head, antenna, apical part of wing, and vein A, unclear and presence or absence of alula unknown.] Vein Sc short and mouth of subcostal cell markedly long; mouth of marginal cell long; vein M_4 arising from discal cell; 4th posterior cell apparently divergent apically. Empodium pad-like. Antenna long and flagellum probably multi-segmented.



Figs 106–107. — *Mesostratiomyia laiyangensis* Hong & Wang (probably in or near Rhagionidae). 106, body; 107, apex of tarsus. From Hong & Wang (1990).

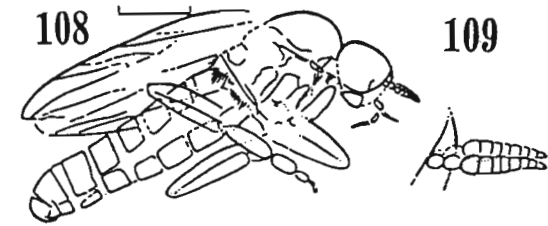
The venation of the apical part of the wing is unknown and family identification is not possible. It can be said roughly that *Mesostratiomyia* is not Stratiomyoidea or Xylophagoidea but Tabanoidea. If so, it would belong in or near Rhagionidae.

Genus *Mongolomyia* Kovalev, 1986, *Trudy Sovmest. Sov.-Mongol. Paleontol. Eksped.*, 28: 142. Type species: *Mongolomyia latitarsis* Kovalev, 1986, by original designation.

latitarsis Kovalev, 1986: 143. Palaeartic: Mongolia (Lower Cretaceous) [Compression or impression].

See figs 108–109 [= Kovalev, 1986: fig. 114a,b].

Body 3.6–4.5 mm and wing 3.0–3.8 mm in length. The details of wing venation are unknown. Antennal flagellum subulate and distinctly 8-segmented. Palpus long, pointed at apex, and with each segment longer than wide. Hind tarsomeres 1–2 each wide and not narrower than hind tibia.



Figs 108–109. — *Mongolomyia latitarsis* Kovalev, ♂ (Stratiomyoidea, Xylophagoidea or Tabanoidea). 108, body; 109, antennae. From Kovalev (1986).

Mongolomyia may belong to Xylomyiidae because of the widened hind tarsomeres 1–2 which may be seen more often in Stratiomyoidea than in Xylophagoidea and Tabanoidea, although its identity also may possibly be a particular family of Xylophagoidea or a particular genus of Rhagionidae or Pelecorhynchidae.

Genus *Shulmas* Kovalev, 1986, *Trudy Sovmest. Sov.-Mongol. Paleontol. Eksped.*, 28: 148. Type species: *Shulmas globiceps* Kovalev, 1986, by original designation.

globiceps Kovalev, 1986: 148. Palaeartic: Mongolia (Lower Cretaceous) [Compression or impression].

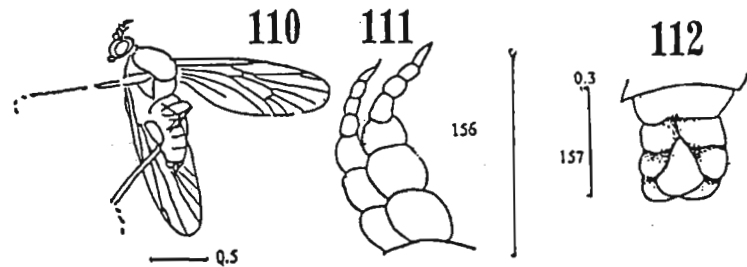
See fig. 96 [= Kovalev, 1986: fig. 119]. *Shulmas globiceps* has the antennal flagellum multi-segmented and with apex pointed. It is certain that *Shulmas* belongs in Stratiomyoidea, Xylophagoidea or Tabanoidea but is not a representative of Rachiceridae, Xylophagidae (s. str.), or Athericidae.

Genus *Stratiomyopsis* Hong & Wang, 1990, *The stratigraphy and palaeontology of Laiyang Basin, Shandong Province*, (Shandong Bureau of Geology and Mineral Resources, China), p. 154. Type species: *Stratiomyopsis robusta* Hong & Wang, 1990, by original designation.

robusta Hong & Wang, 1990: 154. Palaeartic: China (Upper Jurassic) [Compression or impression].

See figs 110–112 [= Hong & Wang, 1990: figs 155–157].

Body 1.5 mm and wing 2 mm in length. Vein Sc weak and not illustrated. Vein R_1 ending opposite middle of wing. Vein R_{2+3} branched and vein R_2 short. Vein R_{4+5} unbranched and ending at wing apex. Fourth posterior cell divergent apically and vein M_4 arising from discal cell. Vein A_1 short [or its apical portion overlooked]. Anal lobe narrow. [Presence or absence of alula unknown.] Mouth of marginal cell markedly wide. Antennal scape and pedicel large and rather quadrate; flagellum distinctly 5-segmented, tapering apically, pointed at apex and with flagellomere 1 widened. Female cercus probably 2-segmented and with apical segment curved inward and pointed at tip.



Figs 110–112. — *Stratiomyopsis robusta* Hong & Wang, ♀ (Brachycera other than Empidoidea + Cyclorrhapha). 110, body; 111, antennae; 112, apex of ♀ abdomen. From Hong & Wang (1990).

The wing venation of *Stratiomyopsis* is peculiar and cannot be placed in any known family. When more material or more accurate knowledge is gained, a new family status would be established for this genus. Its superfamily assignment is difficult. It belongs to the Brachycera other than Empidoidea + Cyclorrhapha.

CONCLUSIONS

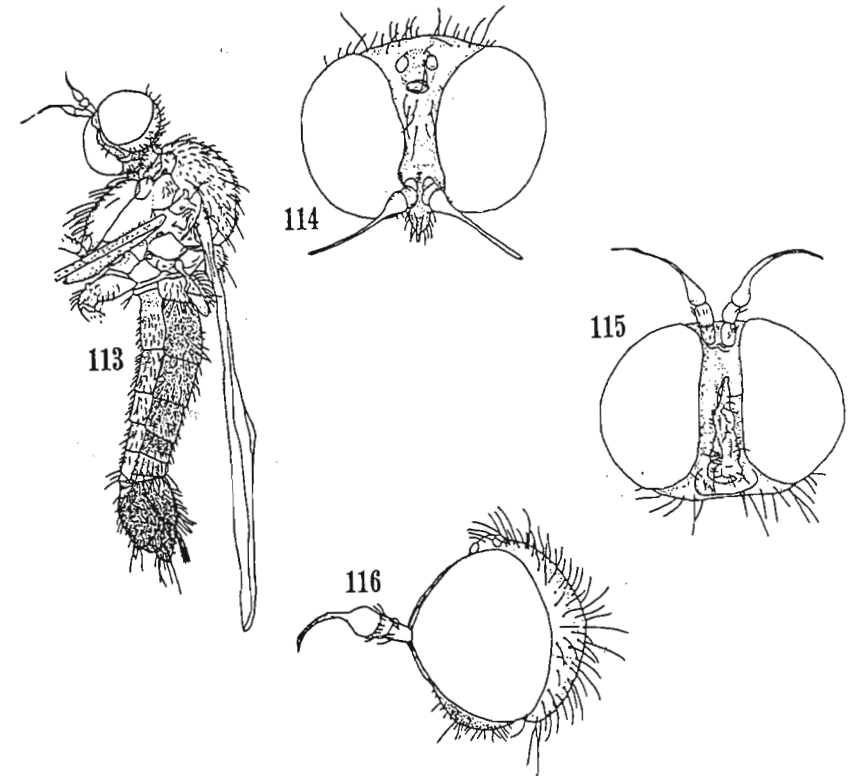
Possible kinships

Several possible kinships are summarized below.

(1) Stratiomyidae, Protomphralidae and the genus *Batgana*: Protomphralidae would be most closely related to Stratiomyidae, if the empodium were pad-like, but the former is at once distinguished from the latter by having basal section of Rs conspicuously long. The definitely known Mesozoic Stratiomyidae is *Cretaceogaster* only. *Batgana* most closely resembles Stratiomyidae in appearance but its exact position is still undetermined because the wing venation is unclear.

(2) Xylomyidae and Zhangsolvidae: No Mesozoic Xylomyidae are known. *Zhangsolva* (= *Archisolva* J. Zhang, S. Zhang & Li, 1993) was placed in Xylomyidae but the Zhangsolvidae has been erected for it, because of the markedly long basal section of Rs and 12-segmented antennal flagellum. Zhangsolvidae may form a stem group of Xylomyidae or that of Stratiomyoidea.

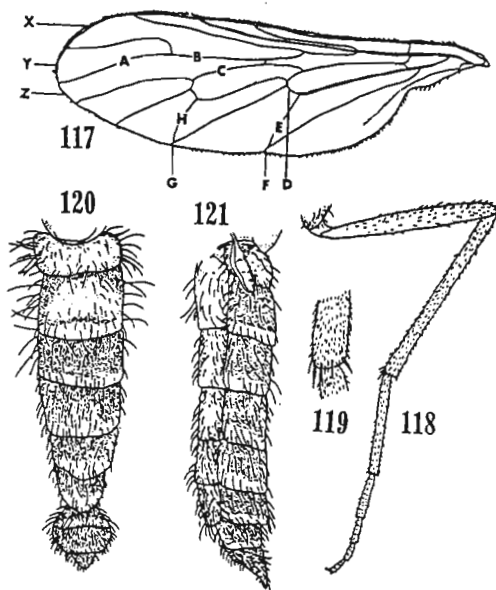
(3) Alinkidae: Judging from antenna, wing venation and female cercus (which is 2-segmented and not dilated posterolaterally), Alinkidae is certainly neither Stratiomyidae nor Tabanoidea. It may form a stem group of Stratiomyoidea + Pantophthalmidae + Xylophagoidea. It is the oldest Brachycera known up to the present.



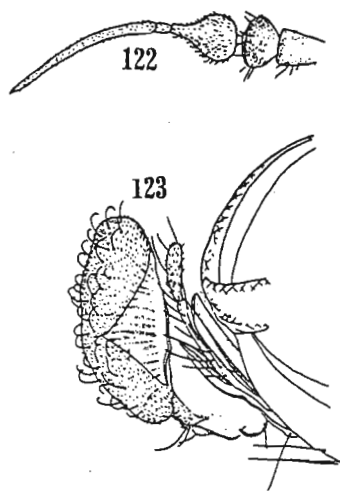
Figs 113–116. — *Apsilocephala longistyla* Kröber, ♂ (living Rhagionempididae). 113, body, lateral view; 114, head, direct frontal view; 115, head, facial view; 116, head, lateral view. From Nagatomi *et al.* (1991a).

(4) Genera *Mesomphrale* and *Stratiomyopsis*: There is no kinship between these two genera. Each of them has an astonishingly curious wing venation and cannot be placed in any known family or superfamily, although it belongs to the Brachycera other than Empidoidea + Cyclorrhapha. A new family status could be established, when more material or more accurate knowledge is gained for each of them.

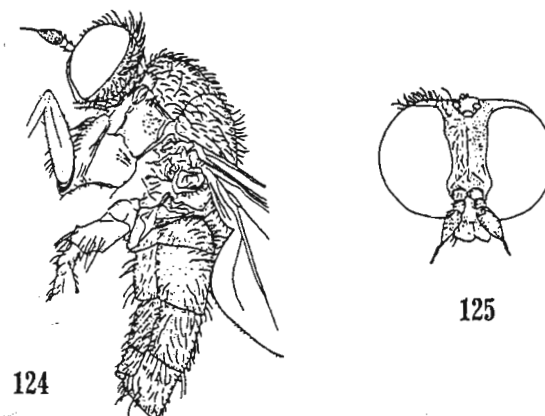
(5) Rhagionidae, Pelecorhynchidae and Eostratiomyiidae: The only reliable distinguishing character between Rhagionidae and Pelecorhynchidae is found in the larval stage only. So no definite Mesozoic Pelecorhynchidae have been identified. Eostratiomyiidae would be identical with either Rhagionidae or Pelecorhynchidae, if the crossveins in the marginal-, 1st submarginal- and 1st posterior cells are abnormal in condition. However, the presence of the r-r crossvein is possibly significant.



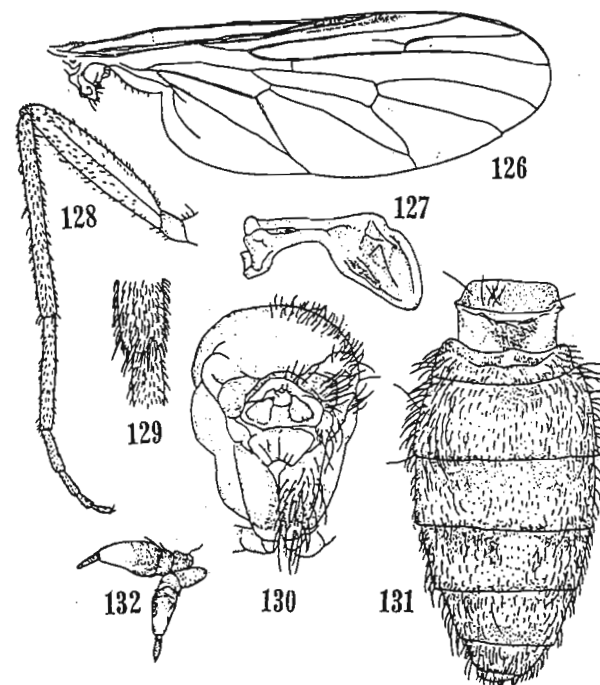
Figs 117–121. — *Apsilocephala longistyla* Kröber (living Rhagionempididae). 117, ♂ wing; 118, ♂ hind leg, anterior view; 119, apex of tibia and base of tarsus in ♂ hind leg; 120–121, ♀ abdomen, dorsal and lateral views. From Nagatomi *et al.* (1991a).



Figs 122–123. — *Apsilocephala longistyla* Kröber, ♂ (macerated in KOH solution) (living Rhagionempididae). 122, antenna (excluding base of scape), outer view; 123, mouthparts and part of head, lateral view. From Nagatomi *et al.* (1991a).



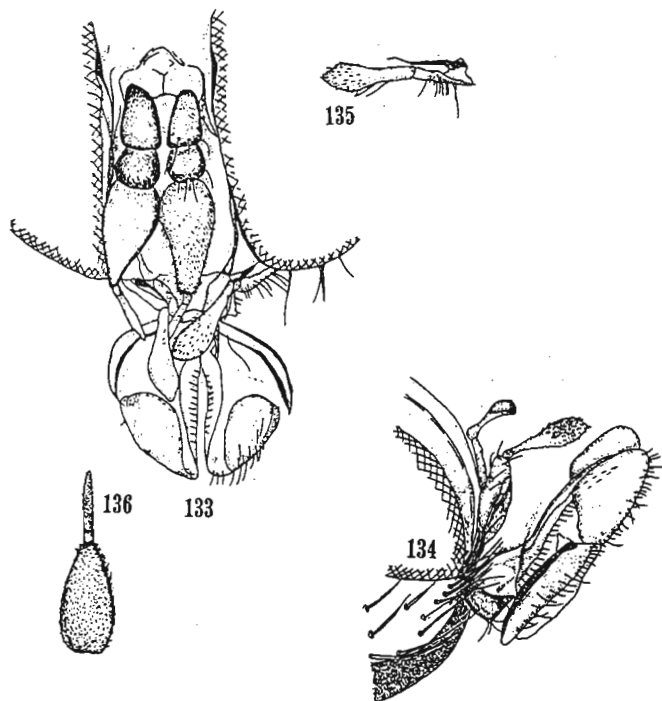
Figs 124–125. — *Clesthentia* sp., ♀ (living Rhagionempididae). 124, body (whose posterior part is cut off), lateral view; 125, head, in direct frontal view. From Nagatomi *et al.* (1991a).



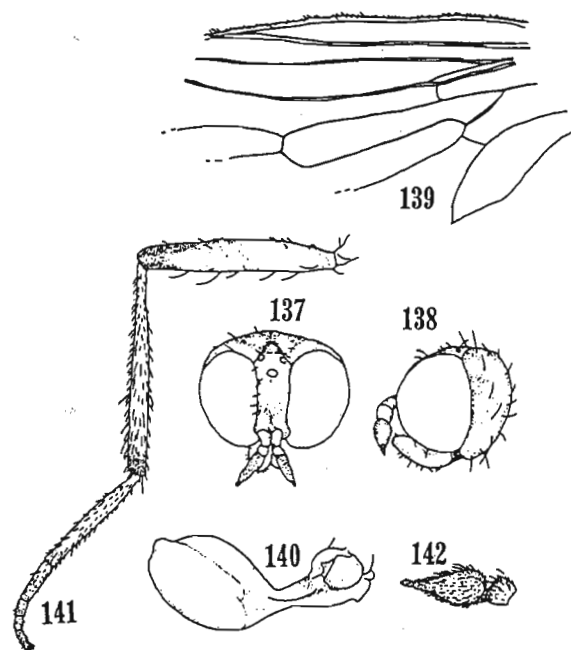
Figs 126–132. — *Clesthentia* sp. (living Rhagionempididae). 126, ♀ wing; 127, ♀ halter, posterior view; 128, ♀ hind leg, posterior view; 129, apex of tibia and base of tarsus of ♀ hind leg, posterior view; 130, ♀ mesonotum, prothorax, fore coxae, etc., anterior view; 131, ♀ scutellum, postscutellum and abdomen, dorsal view; 132, ♂ antennae. From Nagatomi *et al.* (1991a).

(6) Genera *Mesorhagiophryne* and *Mesostratiomyia*: The antenna is unknown in the former genus and apical part of wing is unknown in the latter. Crossvein m-cu arises from vein R_4 and 2nd submarginal cell is conspicuously long in *Mesorhagiophryne robusta* (the type species). Vein Sc is short and mouth of subcostal cell is markedly long in *Mesostratiomyia laiyangensis*. They are unplaced here to a proper family but probably belong in or near Rhagionidae.

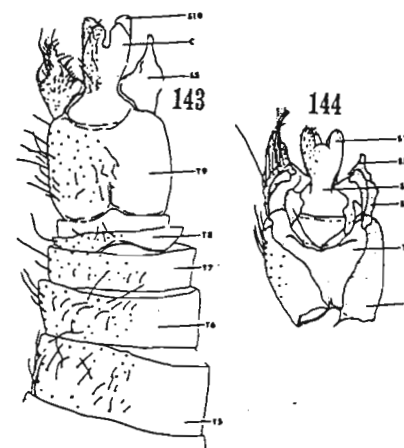
(7) Eomyiidae and the genera *Ija*, *Mongolomyia* and *Shulmas*: The wing venations are unknown and identification is thus not possible, but the proximal part of the wing of *Ija* is present. *Ija* almost certainly represents Xylophagoidea or Pelecorhynchidae of Tabanoidea, because of the short vein Cu_1 . *Mongolomyia* and *Shulmas* belong in Stratiomyoidea, Xylophagoidea or Tabanoidea because of the multi-segmented antennal flagellum. In Eomyiidae, wing venation and antennal structure are not clear. So its definite position cannot be determined.



Figs 133–136. — *Clesthenia* sp., ♀ (macrated in KOH solution) (living Rhagionempididae). 133–134, mouthparts and part of head, dorsal and lateral views; 135, palpus and lacinia (not straightened out), antero-dorsal view; 136, antennal flagellum and style, outer view. From Nagatomi *et al.* (1991a).



Figs 137–142. — *Clestheniella crassioecipitis* Nagatomi, (A.), Saigusa, Nagatomi (H.) & Lyneborg, ♀ (living Rhagionempididae). 137, head, direct frontal view; 138, head, lateral view; 139, part of wing; 140, halter, anterior view; 141, hind leg, anterior view; 142, antennal pedicel, flagellum and style, outer view. From Nagatomi *et al.* (1991a).

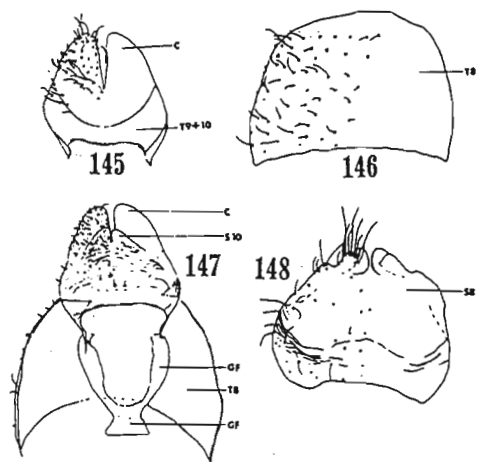


Figs 143–144. — *Apsilocephala longistyla* Kröber, ♂ (living Rhagionempididae). 143, posterior part of abdomen, dorsal view (specimen No. 1); 144, sternum 10, surstyli, and tergum 9, ventral view (specimen No. 2). C, Cercus; SS, surstylus. From Nagatomi *et al.* (1991c).

(8) Vermileonidae and Protobranchycteridae: No definite Mesozoic Vermileonidae are known. Only wing is known in Protobranchycteridae where wing form is wide and vein Cu_1 is long relative to those of Vermileonidae. It is difficult to determine the position of Protobranchycteridae on the basis of wing only. However, the Protobranchycteridae is placed here near Vermileonidae until more knowledge is gained.

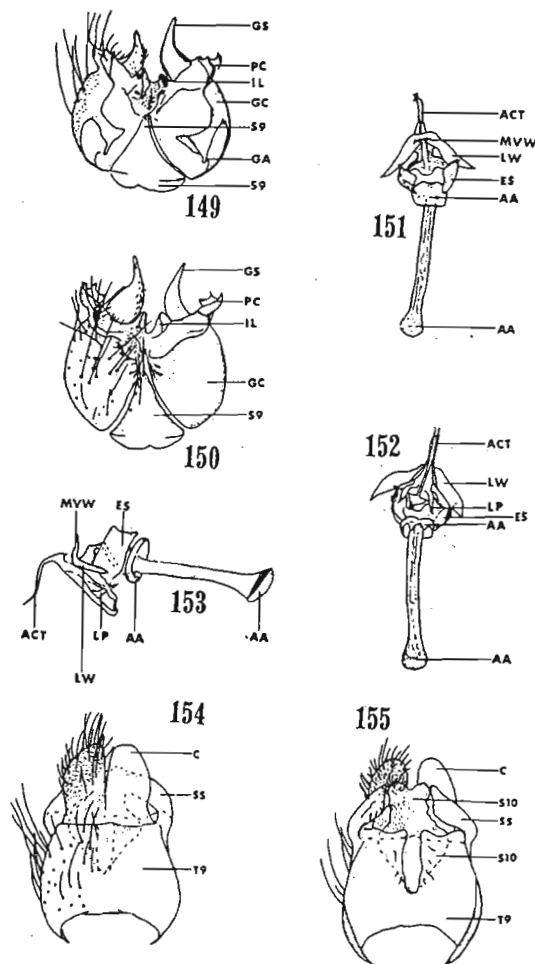
(9) Nemestrinidae, Archisargidae and Eremochaetidae: A kinship is almost certain and the above 3 families are grouped together here. A needle-like ovipositor is seen in *Mesosolva* (Archisargidae), *Eremochaetosoma* (Eremochaetidae), and several genera of Nemestrinidae, although the presence or absence of this type of ovipositor varies with genus in Nemestrinidae. In Nemestrinidae and Eremochaetidae, part of R veins are usually anastomosed with discal cell. For a relation between Archisargidae and Eremochaetidae, see notes under Archisargidae.

(10) Apsilocephalidae and Rhagionempididae: No significant difference is found between living Apsilocephalidae and extinct Rhagionempididae. The Apsilocephalidae would be identical with Rhagionempididae, if Gen. et sp. 1 by Kovalev (1986) is a true Rhagionempididae and its posterolateral process (fig. 53) on male tergum 9 represents surstylus. The Apsilocephalidae is here treated as a new junior synonym of Rhagionempididae, because this may emphasise more strongly in future study the true relationship between them. For comparative purposes, several illustrations (figs 113–160) of living Rhagionempididae (= Apsilocephalidae) are reproduced here from Nagatomi *et al.* (1991a,c).



Figs 145–148. — *Apsilocephala longistyla* Kröber, ♀ (living Rhagionempididae). 145, cerci and tergum 9+10, dorsal view; 146, tergum 8, dorsal view; 147, cerci, sternum 10, tergum 8, and genital fork, ventral view; 148, sternum 8, ventral view. C, cercus; GF, genital fork. From Nagatomi *et al.* (1991c).

(11) Empididae and Protempididae: Protempididae is easily separated from Rhagionempididae as shown in the key (4) (couplet 15, p. 102). It appears that Protempididae is more similar phylogenetically to Empididae + Dolichopodidae than to Rhagionempididae.



Figs 149–155. — Male genitalia of *Clesthentia* sp. (living Rhagionempididae). 149, 151 and 154, dorsal view; 150, 152 and 155, ventral view; 153, lateral view. AA, Ejaculatory apodeme; ACT, apical conical tube; C, cercus; ES, lateral ejaculatory process (= endophallic sclerite); GA, gonocoxial apodeme; GC, gonocoxite; GS, gonostylus; IL, inner lobe of apical patch of gonocoxite; LP, lateral process of ventral plate; LW, lateral wing of dorsal plate; MVW, mid-ventral wing of dorsal plate; PC, posterolateral crest of gonocoxite; SS, surstylus. From Nagatomi *et al.* (1991c).

TABLE 1. — GENERA SHOWING CHANGE OF FAMILY ASSIGNMENT FROM EVENHUIS (1994) TO THE PRESENT

Genus	Evenhuis (1994)	Present article
<i>Archirhagio</i>	Rhagionidae	Archisargidae
<i>Archisargus</i>	Eremochaetidae	"
<i>Ija</i>	Rhagionidae	[Unplaced to proper family]
<i>Mesomphrale</i>	Protomphralidae	"
<i>Mesorhagiophryne</i>	Rhagionidae	"
<i>Mesosolva</i>	[Unplaced Brachycera]	Archisargidae
<i>Mesostratiomyia</i>	Rhagionidae	[Unplaced to proper family]
<i>Mongolomyia</i>	"	"
<i>Stratiomyopsis</i>	"	"
<i>Palaeophora</i>	[Unplaced Brachycera]	Palaeophoridae
<i>Prosolva</i>	"	Archisargidae
<i>Zhangsolva</i>	Xylomyidae	Zhangsolvidae
Gen. et sp. 1*	Rhagionidae	Rhagionempididae

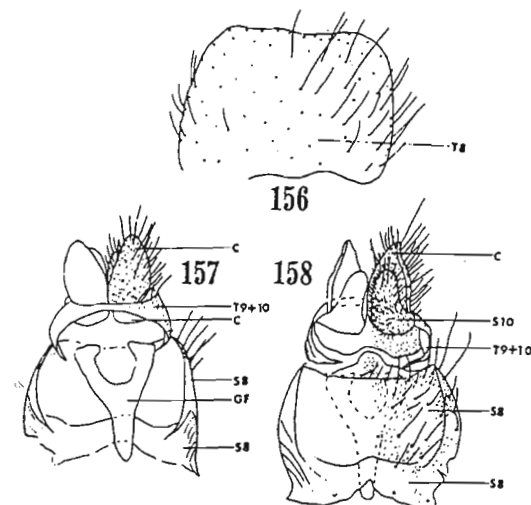
*The genus, questionably placed in Rhagionidae by Kovalev (1986), was not mentioned by Evenhuis (1994).

TABLE 2. — MESOZOIC FOSSIL RECORD OF LIVING FAMILIES IN BRACHYCERA (SPECIES NUMBER/GENUS NUMBER). PREPARED AND MODIFIED FROM EVENHUIS (1994). A, EXTINCT GENERA; B, LIVING GENERA.

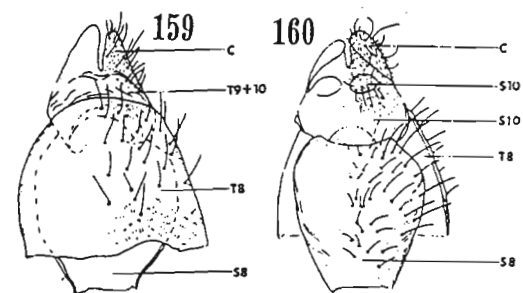
Super-family	Family		Middle Jurassic	Upper Jurassic	Lower Cretaceous	Upper Cretaceous
1	Stratiomyidae (Parhadrestiinae)	A				1/1
3	Rhagionidae	A B	2/2	10/6	2/2 3/3	1/1
4	Nemestrinidae	A		8/5 (1/1)		
	Acroceridae	A		1/1		
5	Bombyliidae (Mythicomyiinae)	A	1/1			2/2
	Asilidae	A				1/1
6	Rhagionempididae (= Apsilocephalidae)	A	2/2	2/2	1/1	
	Empididae	A B		(2/2)	2/2	8/7 1/1
	Platyezidae	A			6/5*	
	Ironomyiidae	A				1/1
	Phoridae	A B				5/2 1/1
	Calliphoridae	A				1/1

Notes:

- (a) 1, Stratiomyoidea + Pantophthalmidae; 2, Xylophagoidea; 3, Tabanoidea; 4, Nemestrinoidea; 5, Asiloidea; 6, Empidoidea + Cyclorhapha and its ancestral forms.
 (b) Middle/Upper Jurassic and Upper Jurassic/Lower Cretaceous are treated as Upper Jurassic and Lower Cretaceous respectively.
 (c) Genera questionably placed by Evenhuis are shown in parentheses.
 (d)* Contrary to Evenhuis (1994), the age of Layian Formation is considered here as Lower Cretaceous (not Upper Jurassic).



Figs 156–158. — Female genitalia of *Clesthentia* sp. (living Rhagionempididae). 156–157, dorsal view; 158, ventral view. C, cercus; GF, genital fork. From Nagatomi *et al.* (1991c).



Figs 159–160. — Female genitalia of *Clesthentiella crassiocipitis* Nagatomi (A.), Saigusa, Nagatomi (H.) & Lyneborg (living Rhagionempididae). 159, dorsal view; 160, ventral view. C, cercus. From Nagatomi *et al.* (1991c).

Notes on Tables 1–4

Table 1 shows the genera whose family assignment has altered from Evenhuis (1994) to the present.

Tables 2–3 have been prepared and modified from Evenhuis (1994) and the following may be learned from them. Further, Table 4 is appended. Questionably placed genera by Evenhuis (1994) have been included in each family.

- (1) Upper Triassic: Alinkidae.
- (2) Lower Jurassic: Protobranchyoceridae.
- (3) Middle Jurassic: Rhagionidae; Archisargidae; Bombyliidae (Mythicomyiinae); Rhagionempididae.
- (4) Upper Jurassic: Rhagionidae (6 genera and 10 species); Archisargidae (2 genera and 2 species); Eremochaetidae (2 genera and 2 species); Nemestrinidae (6 genera and 9 species); Rhagionempididae (2 genera and 2 species); Empididae (2 genera and 2 species); etc.
- (5) Nemestrinoidea: 4 families, 15 genera and 18 species are known to date.
- (6) Asiloidea: Except for Bombyliidae (Mythicomyiinae) (3 genera and 3 species), only 1 genus and 1 species of Asilidae are known to date.
- (7) Empidoidea + Cyclorrhapha and its ancestral forms: 9 families, 30 genera and 35 species are known to date.
- (8) No definite Mesozoic Xylophagoidea have been described. The heyday of Xylophagoidea was possibly absent or short and quickly replaced by the activity of Rhagionidae.

TABLE 3. — MESOZOIC FOSSIL RECORD OF EXTINCT FAMILIES OR GENERA IN BRACHYCERA. PREPARED AND MODIFIED FROM EVENHUIS (1994).

Super-family	Family or genus	Upper Triassic	Lower Jurassic	Middle Jurassic	Upper Jurassic	Lower Cretaceous
1	Protomphralidae <i>Baigana</i> Zhangsolvidae				1/1	1/1
1+2*	Alinkidae	1/1				
1, 2 or 3	<i>Mongolomyia</i> <i>Shulmas</i>					1/1 1/1
1, 2, 3 or 4	Eomyiidae				1/1	
1 to 5**	<i>Mesomphrale</i> <i>Stratiomyopsis</i>				1/1 1/1	
2 or 3	<i>Ija</i>			1/1		
3	Eostratiomyiidae <i>Mesorhagiophryne</i> <i>Mesostratiomyia</i>				1/1 2/1 1/1	
4	Archisargidae Eremochaetidae			2/2	2/2 2/2	2/2
6	Protobranchyoceridae Protempididae		1/1		1/1	
?	Palaeophoridae				1/1	

Notes: (a) and (b) in Table 1 are applicable here. *[1+2] means an ancestral form of Stratiomyoidea + Xylophagoidea. **[1 to 5] means the Brachycera other than Empidoidea + Cyclorrhapha.

TABLE 4. — CENOZOIC FOSSIL RECORD OF ORTHORRHAPHOUS BRACHYCERA (SPECIES NUMBER/GENUS NUMBER). PREPARED FROM EVENHUIS (1994). A, EXTINCT GENERA; B, LIVING GENERA.

Super-family	Family	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
1	Stratiomyidae	A	1/1	4/4				
	Xylomyidae	B		11/9 3/2	2/2		1/1	
2	Rachiceridae	A		3/3				
		B		1/1				
	Xylophagidae	A		2/2				
		B		2/1				
	Coenomyiidae (<i>Dialysis</i>)	B		1/1				
3	Rhagionidae	A			(1/1)			
		B		24/4				
	Athericidae	A		2/1				
		B		2/2				
	Tabanidae	A		1/1				
		B		8/4	2/1	[1/1]*	1/1	
4	Nemestrinidae	B		5/3				
	Acroceridae	A		4/4				
		B		1/1				
5	Bombyliidae (Mythicomyiinae)	B		1/1	[2/1]*			
	Bombyliidae (except Mythicomyiinae)	A		16/12 (1/1)				
		B		27/18	1/1 [3/2]*		1/1	
	Therevidae	A	(1/1)	1/1				
		B		7/4	[2/2]*			
	Scenopinidae	B			1/1			
	Mydidae	B		1/1				
	Asilidae	A	2/2	2/2				
		B	1/1	25/17 [7/1]*	4/3 [6/2]*	1/1		
	6	Vermileonidae	A		1/1			
Empididae		A	2/2	11/11	1/1 (1/1)			
		B	2/2	58/21 [30/1]*	1/1 [1/1]*	[1/1]*		
Dolichopodidae		A	4/2	11/5				1/1
	B	1/1	54/17 [10/1]*				[1/1]*	

Notes: (a), (b) and (c) in Table 1 are applicable here. The genus based on unidentified sp. is included in the number of genus but the unidentified sp. is excluded from the number of species per genus. *The genus number in brackets is duplicated with that shown in other rank or epoch (for example in Tabanidae, one of the 4 genera found in Oligocene is also found in Pliocene).

ACKNOWLEDGEMENTS

This paper is dedicated to Dr Neal L. Evenhuis (Honolulu) who catalogued the fossil Diptera in 1994. Grateful acknowledgements are made to the previous authors whose illustrations have been borrowed here; the present paper would have little value without the figures quoted. It also commemorates Professor Katsura Morimoto (Fukuoka) for his active career and retirement from Kyushu University in 1997. Our deep appreciation is expressed to Mr K.G.V. Smith (London) and anonymous referees for critical reading of the manuscript.

[For References see p. 190]

APPENDIX I

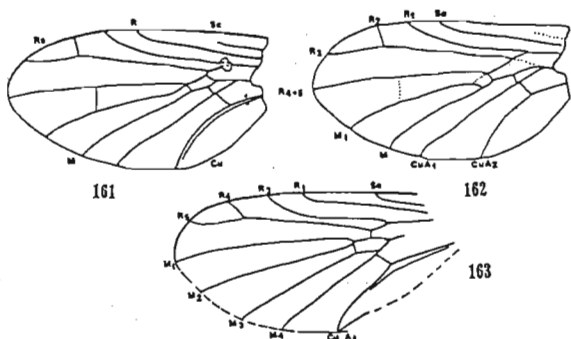
Ansorge & Krzemiński (1994) on the family Oligophrynidae (= Oligophryneidae) Rohdendorf, 1962 (with 1 genus) must be introduced. The Lower Jurassic *Oligophryne*, placed by Evenhuis (1994) in Anisopodidae, is apparently most closely related to the members of Stratiomyidae. If so, the origin of a stem group of Stratiomyidae (not Stratiomyoidea) would go back at least to the Lower Jurassic.

FAMILY OLIGOPHRYNIDAE

Genus *Oligophryne* Rohdendorf, 1962, [*Fundamentals of palaeontology*], Vol. 9: 332. Type species: *Oligophryne fungivoroides* Rohdendorf, 1962, by original designation.

See figs 163–165 (= Ansorge & Krzemiński, 1994: figs 3–5).

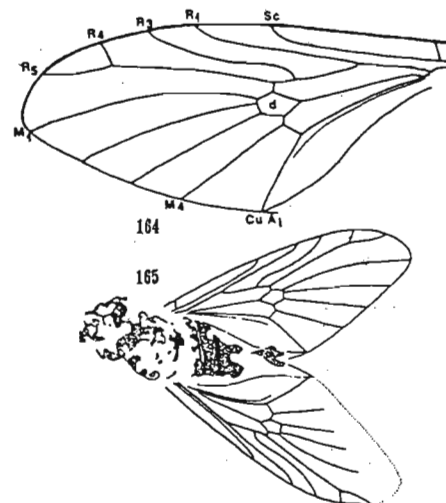
Vein R_5 ending far above wing apex; vein Sc situated opposite at or near r-m crossvein; basal section of Rs long relative to that of Stratiomyidae; mouth of subcostal cell roughly as long as wing margin between R_1 and R_4 ; mouth of 2nd submarginal cell not shorter than that of 1st submarginal cell; vein R_4 short; 5 posterior cells present; 4th posterior cell divergent apically; anal cell closed at wing margin; discal cell small; 4 M veins long; [anal lobe of wing and presence or absence of alula unclear or unknown].



Figs 161–163. — *Oligophryne fungivoroides* Rohdendorf (Oligophrynidae). 161, After Rohdendorf (1964); 162, after Amorim (1992); 163, after Ansorge & Krzemiński (1994). From Ansorge & Krzemiński (1994).

Oligophryne falls in the upper branch of couplet 5 of key (4), but may be separated from *Protomphrale* by having vein R_3 long, and basal section of Rs short. [In *Protomphrale*, venation is unknown on the posterior part of wing.] It is easily separated from *Cretaceogaster* (Stratiomyidae: Parhadrestiinae) by having the following characters:

mouth of subcostal cell long; mouth of marginal cell nearly as long as that of 1st submarginal cell; basal section of Rs distinctly over $1/2$ as long as distance between humeral crossvein and base of Rs (at least in *britannica*); 5 posterior cells (or 4 M veins) present; discal cell small and M veins long; vein M_4 arising from 2nd basal cell; anal cell closed at wing margin.



Figs 164–165. — *Oligophryne britannica* Ansorge & Krzemiński (Oligophrynidae). From Ansorge & Krzemiński (1994).

Ansorge & Krzemiński (1994: 119) wrote,

“Two characters of wing venation place this family in the Oligoneura Brachycera: very long R_{4+5} with very short R_3 and A_1 terminating close or in the Cu tip. This combination of characters is never present in the Nematocera. The small d cell may indicate the closeness of this family to the Stratiomyidae (infraorder Stratiomyomorpha).”

britannica Ansorge & Krzemiński, 1994, *Acta zool. cracov.*, 37(2): 117.

Palearctic: England (Lower Jurassic) [Compression or impression].

See figs 164–165. Body c. 3.2 mm and wing 3 mm in length. Wing apex bluntly pointed; discal cell “broadly pentagonal”; space between discal cell and base of M_4 distinct.

fungivoroides Rohdendorf, 1962: 332. Palearctic: Kirghizstan (Lower Jurassic) [Compression or impression].

See fig. 163 (= Ansorge & Krzemiński, 1994: fig. 3 based on holotype). The wing venation in figs 161–162 was misinterpreted by Rohdendorf

(1964) and Amorim (1992) respectively. Wing (without proximal part) c. 1.8 mm in length. "Entire wing length could reach approximately 2.4 mm." (after Ansoorge & Krzemiński, 1994: 116). Wing apex rounded; discal cell pentagonal and elongate; space between discal cell and base of M_4 short and inconspicuous.

APPENDIX II

Knowledge is progressing rapidly and the foregoing account has become out of date.

The works subsequent to Evenhuis (1994), by Mostovski (1996a,b, 1997) on Archisargidae, Archocyrtidae, Eremochaetidae and Kovalevisargidae must now be introduced. Mostovski places these in the superfamily Archisargoidea. Ren & Guo (1995) on Eremochaetidae is also added.

Based on APPENDIX I & II, Tables 5–7 are given as amendments to Tables 1–3.

TABLE 5. — AMENDMENT FOR TABLE 1 (p. 156)

Genus	Evenhuis (1994)	Present article
<i>Archocyrtus</i>	Acroceridae	Archocyrtidae
<i>Oligophryne</i>	Anisopodidae	Oligophrynidae
<i>Rhagionemestrius</i>	Nemestrinidae	Rhagionemestriidae
<i>Sinonemestrius</i>	"	Sinonemestriidae

TABLE 6. — AMENDMENT FOR TABLE 2 (p. 156)

Super-family	Family	Middle Jurassic	Upper Jurassic	Lower Cretaceous	Upper Cretaceous
4	Nemestrinidae	A	7/4		
	Acroceridae	A	0		

TABLE 7. — AMENDMENT TO STRATIOMYOIDEA AND NEMESTRINOIDEA FOR TABLE 3 (p. 158)

Super-family	Family or genus	Lower Jurassic	Middle Jurassic	Upper Jurassic	Lower Cretaceous
1	Oligophrynidae	A	2/1		
4	Archisargidae	A	2/2*	15/6	
	Archocyrtidae	A		1/1	
	Eremochaetidae	A		5/4	7/3
	Kovalevisargidae	A		2/2	
	Rhagionemestriidae	A		1/1	
	Sinonemestriidae	A		1/1	

*These 2 genera each has the species from Upper Jurassic.

SUPERFAMILY NEMESTRINOIDEA (= Archisargoidea)

It seems that the Archisargoidea is identical with, or most closely related phylogenetically to, the Nemestrinoidea. However, no definite synapomorphic morphological character state has been detected for (a) Nemestrinidae + Acroceridae (= Nemestrinoidea), for (b) Archisargidae + Eremochaetidae + Kovalevisargidae (Archisargoidea of Mostovski, 1997) or for (a) + (b) + Rhagionemestriidae + Sinonemestriidae (Nemestrinoidea here expanded).

It should be noted that the known larvae of Nemestrinoidea are neither scavengers (which are seen in Stratiomyoidea), nor sap feeders (Pantophthalmidae), nor predators (Xylophagoidea and Tabanoidea), but parasites. Bombyliidae (whose larvae are mostly parasites) belong to the Asiloidea (see Woodley, 1989; Nagatomi, 1992, 1996).

KEY 7: (= AMENDMENT FOR KEY 4: MESOZOIC FAMILIES OF BRACHYCERA – P. 100) (BASED ON APPENDIX II)

- 3 Part of R vein anastomosed with discal cell and r-m crossvein absent 4¹
 — R vein independent of discal cell and r-m crossvein present 6¹ (= 4 in key 4)
- 4¹ Vein R_{2+3} present; abdomen slender or more slender relative to that of Archocyrtidae 5¹
 — Vein R_{2+3} absent; abdomen robust; (fig. 218) Archocyrtidae
- 5¹ Costa + vein R_1 markedly thickened and ending at apex of vein R_5 beyond wing tip (fig. 218) Rhagionemestriidae
 — Costa and vein R_1 not as above; (figs 19–26, 190–207) Eremochaetidae
- 6¹ Vein $R_4 + R_5$ forked (or vein R_4 present); vein M_1 arising at or near apex of discal cell 4 (= 4 in key 4)
 — Vein $R_4 + R_5$ unforked (or vein R_4 absent) [this is so in *Stratiomyopsis* put under couplet 8 in key 4]; vein M_1 arising far before apex of discal cell [this is not in *Stratiomyopsis*]; (figs 203–209) Kovalevisargidae
- 4 Vein R_5 ends far above wing apex 5 (= 5 in key 4)
 — Vein R_5 ends at, near or far below wing apex 10 (= 10 in key 4)
- 10 Basal section of R_s gently curved upward at base or nearly straight 11¹
 — Basal section of R_s abruptly curved upward at base; (4th posterior cell with long petiole; vein R_5 ends near [rather above] wing apex; anal cell probably closed or convergent apically; antennal flagellum 12-segmented and with short spine; ovipositor short and triangular); (figs 99–94) Zhangsolvidae
- 11¹ Second posterior cell divergent apically and mouth of 3rd posterior cell shorter than, roughly as long as, or at most about twice as long as, that of 2nd posterior cell 12¹
 — Second posterior cell narrowed apically and mouth of 3rd posterior cell conspicuously widened and much longer than that of 2nd posterior cell; (mouth of subcostal cell apparently short); (fig. 219) Sinonemestriidae
- 12¹ Fourth posterior cell (3rd + 4th posterior cell) usually wide open or sometimes narrowly open 12 (= 12 in key 4)
 — Fourth posterior cell closed far before wing margin; (figs 11–16, 171–179, 182, 184) Archisargidae
 (*Mesosolva*, *Parvisargus* [*malus*] and *Prosolva*)

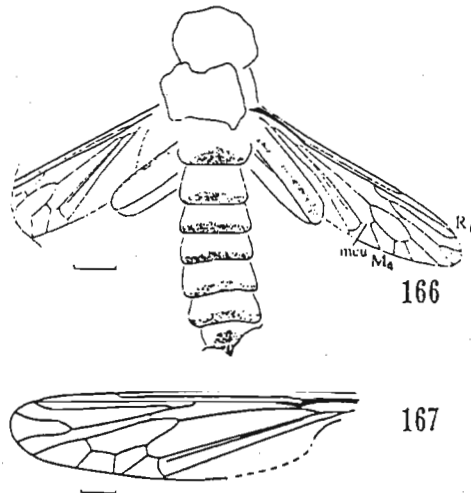
- 12 Wing margin between R_1 and R_4 much longer than mouth of 2nd submarginal cell and usually so than mouth of subcostal cell 13 (= 13 in key 4)
- Wing margin between R_1 and R_4 somewhat shorter than, or sometimes longer than, mouth of 2nd submarginal cell, and shorter than mouth of subcostal cell; (antennal flagellum bristle-like totally or at least apically; abdomen almost parallel-sided; (figs 7–9, 166–170, 180–181, 183, 185–188) Archisargidae (*Archirhagio*, *Archisargus*, *Calosargus*, *Ovisargus*, *Parvisargus* [*peior*] and *Sharasargus*)

FAMILY ARCHISARGIDAE

See p. 105 and keys 4 (p. 100) & 7 (p. 163). Among the Nemestrinoidea, here expanded, the most generalized wing venation is seen in Archisargidae where r-m crossvein is present, vein $R_4 + R_5$ is forked and no diagonal vein is seen. However, several derived features occur within this family: vein R_{2+3} ending at vein R_1 far before wing margin in *Calosargus*; 4th posterior cell closed far before wing margin in *Mesosolva* and *Prosolva*; vein Cu_1 markedly short in *Archisargus*; vein M_3 absent in *Ovisargus*, *Sharasargus* and *Calosargus* (*Calosargus*).

There are possible synapomorphic character states for this family: antennal flagellum entirely bristle-like (if the widened part before arista is not the flagellomere 1 but the pedicel, as in many [not all] genera of Eremochaetidae; abdomen slender, almost parallel-sided, and with needle-like ovipositor (as in Eremochaetidae); hind leg markedly long (as in Eremochaetidae).

If presence or absence of r-m crossvein proves to have no significance as a family character, Eremochaetidae would become a junior synonym of Archisargidae.



Figs 166–167. — *Archisargus* spp. (Archisargidae). 166, *A. pulcher* Rohdendorf; 167, *A. maximus* Mostovski. From Mostovski (1997).

Genus *Archisargus* Rohdendorf: see p. 106.

pulcher Rohdendorf: see p. 106–7.

See fig. 166 (= Mostovski, 1997: fig. 1a). Body 16 mm and wing 12 mm in length. Mouth of subcostal cell longer than wing margin between R_1 and R_5 . Marginal cell narrowly open (or nearly closed). Vein R_5 ending behind wing apex. r-m crossvein present. Fourth posterior cell convergent apically but wide open. Vein Cu_1 markedly short. Anal cell closed slightly before wing margin. r-m crossvein situated about at middle of discal cell.

maximus Mostovski, 1997, *Paleontol J.*, 1997 (No. 1): 74. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

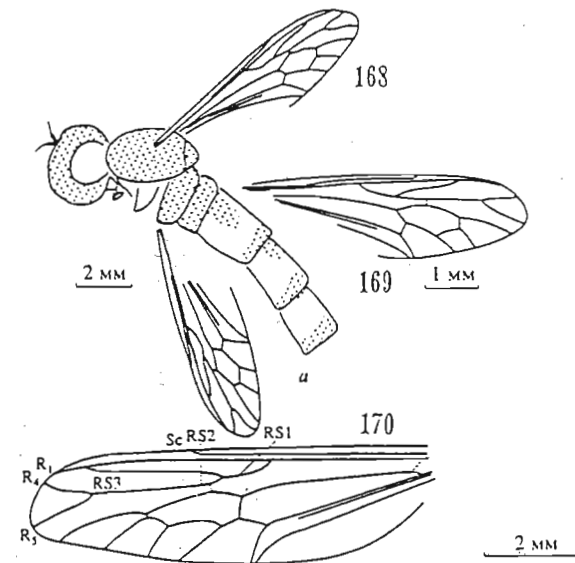
See fig. 167 (= Mostovski, 1997: fig. 1b). Wing 20 mm in length. Second submarginal cell and discal cell apparently longer than in *pulcher*: r-m crossvein situated at basal part of discal cell.

Genus *Calosargus* Mostovski, 1997, *Paleontol J.*, 1997 (No. 1): 74. Type species: *Calosargus tatianae* Mostovski, 1997, by original designation.

Similar to *Archisargus* but differing from the latter in the following respects:

vein R_{2+3} ending at vein R_1 far before wing margin; vein M_4 arising from discal cell; vein M_3 absent in *Calosargus* (*Calosargus*); anal cell narrowly open; vein Cu_1 short but distinctly longer than in *Archisargus*.

tatianae Mostovski, 1997, *Paleontol J.*, 1997 (No. 1): 75. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].



Figs 168–170. — *Calosargus* spp. (Archisargidae). 168, *C. (C.) tatianae* Mostovski; 169, *C. (C.) niger* Mostovski; 170, *C. (Pterosargus) thanasymus* Mostovski. From Mostovski (1997).

See fig. 168 (= Mostovski, 1997: fig. 2a). Wing 8.5 mm in length. Antennal flagellum bristle-like totally (if widened part just before arista represents pedicel). Vein M_3 absent. Vein M_4 arising from apical portion of discal cell.

niger Mostovski, 1997, *Paleontol J.*, 1997 (No. 1): 75. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 169 (= Mostovski, 1997: fig. 2b). Body 15.5 mm and wing 7 mm in length. Discal cell and mouth of 2nd posterior cell apparently longer than in *tatiana*.

Subgenus *Calosargus* (*Pterosargus*) Mostovski, 1997, *Paleontol J.*, 1997 (No. 1): 74. Type species: *Calosargus* (*Pterosargus*) *thanasymus* Mostovski, 1997, by original designation.

thanasymus Mostovski, 1997, *Paleontol J.*, 1997 (No. 1): 74. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 170 (= Mostovski, 1997: fig. 2c). Wing 8 mm in length. Vein M_3 present and complete. Vein M_4 arising from basal portion of discal cell. Veins M_1 and M_2 apparently longer than in *Calosargus* (*Calosargus*), that is, *tatiana* and *niger*.

Genus *Mesosolva* Hong: see p. 107.

parva Hong: see p. 107–8.

The type species of *Mesosolva* (= *M. parva*) differs from that of *Prosolva* (= *P. huabeiensis*) in the following respects:

(1) anal cell parallel-sided apically; (2) mouth of subcostal cell somewhat shorter than wing margin between R_1 and R_2 , and (3) vein R_3 about as long as 2nd section of $R_1 + R_2$. In *P. huabeiensis*, (1) divergent apically, (2) distinctly longer, and (3) much shorter. Mostovski (1996a) added 7 new species to *Mesosolva*. The specific variation occurs at least in the characters (2) and (3) above.

The new species described by Mostovski (1996a) are as follows: Kazakhstan (Upper Jurassic): *angustocellulata*; *balyshvae*; *dolosa*; *hennigi*; *imperfecta*; *rohdendorfi*. Mongolia (? Upper Jurassic): *longivena*. They are shown in figs 171–179 (= Mostovski, 1996a: fig. 1a–e & fig. 2a–d) and key 9.

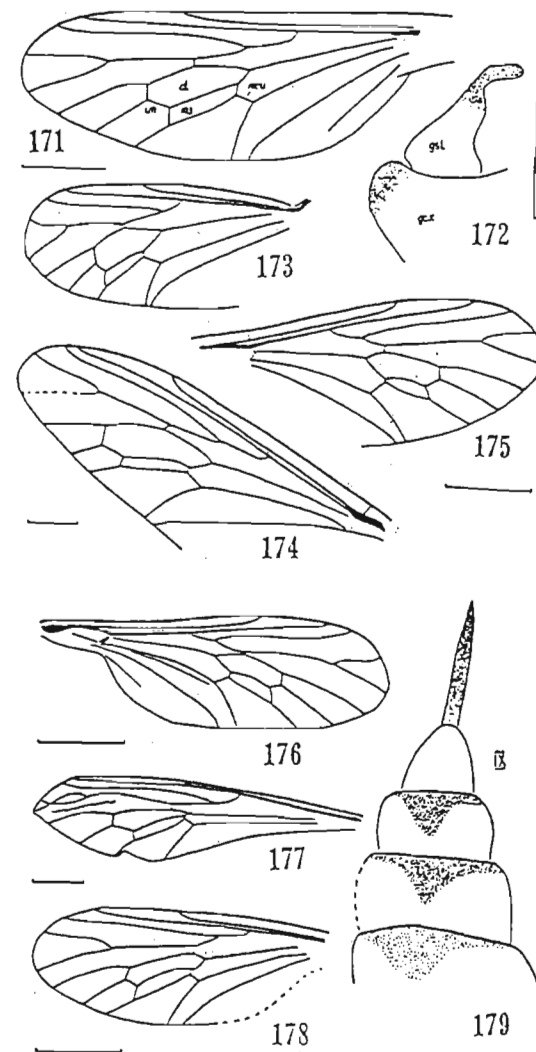
Genus *Ovisargus* Mostovski, 1996b, *Russian Entomol. J.*, 5: 121. Type species: *Ovisargus gracilis* Mostovski, 1996, by original designation. *gracilis* Mostovski, 1996b, *Russian Entomol. J.*, 5: 121. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See figs 180–181 (= Mostovski, 1996b: figs 15–16). Body 11.7 mm and wing 6 mm in length. Body slender and ovipositor needle-like. Posterior cells 4 in number. Vein M_3 absent and vein M_4 arising from apical portion of discal cell (it is interpreted also that vein M_3 is present but vein M_4 absent). Anal cell closed before wing margin. Mouth of marginal cell open and not narrowed apically. Vein R_4 short and 2nd submarginal cell small. Mouth of subcostal cell nearly as long as wing margin between R_1 and R_2 .

Genus *Parvisargus* Mostovski, 1996b, *Russian Entomol. J.*, 5: 122. Type species: *Parvisargus malus* Mostovski, 1996, by original designation.

Very similar to *Archisargus* but differing from the latter in the following respects:

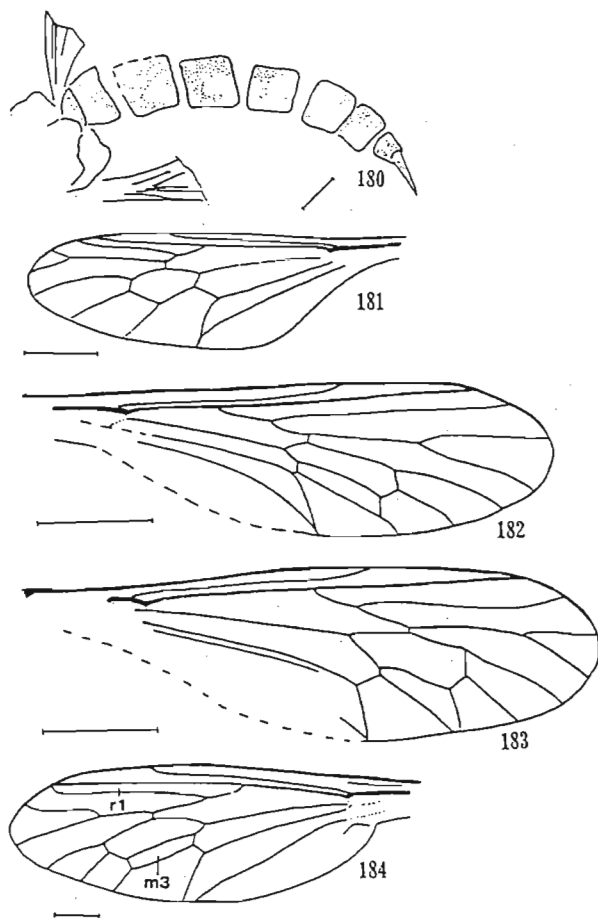
marginal cell wide open and not narrowed apically; 4th posterior cell and vein Cu_1 distinctly longer than in *Archisargus* (compare figs 182–183 with figs 166–167).



Figs 171–179. — *Mesosolva* spp. (Archisargidae). 171–172, *M. rohdendorfi* Mostovski (gcx, gonocoxite; gst, gonostylus); 173, *M. hennigi* Mostovski; 174, *M. angustocellulata* Mostovski; 175, *M. dolosa* Mostovski; 176, *M. longivena* Mostovski; 177, *M. imperfecta* Mostovski; 178–179, *M. balyshvae* Mostovski (179, female terminalia). Scale bar = 1 mm (172, 0.25 mm; 179, 0.5 mm). From Mostovski (1996a).

malus Mostovski, 1996b, *Russian Entomol. J.*, 5: 123. Palearctic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 182 (= Mostovski, 1996b: fig. 17). Wing 4.6 mm in length. Fourth posterior cell closed far before wing margin. Basal section of Rs roughly $\frac{1}{2}$ (or over $\frac{1}{2}$) as long as that of R (= distance between base of 1st basal cell and base of marginal cell). r-m crossvein situated at basal part of discal cell. Vein R_4 about as long as 2nd section of $R_4 + R_5$. m-cu crossvein short. Mouth of subcostal cell somewhat shorter than wing margin between R_1 and R_5 . Anal cell closed before wing margin.



Figs 180–184. — Archisargidae. 180–181, *Ovisargus gracilis* Mostovski, ♀ (180, abdomen, etc.); 182, *Parvisargus malus* Mostovski; 183, *Parvisargus peior* Mostovski; 184, *Prosolva(?) karataviensis* Mostovski. Scale bar = 1 mm. From Mostovski (1996b).

peior Mostovski, 1996b, *Russian Entomol. J.*, 5: 123. Palearctic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 183 (= Mostovski, 1996b: fig. 18). Wing 5 mm in length. Fourth posterior cell convergent apically but wide open. Basal section of Rs roughly $\frac{1}{4}$ as long as that of R. r-m crossvein situated at middle of discal cell. Vein R_4 distinctly shorter than 2nd section of $R_4 + R_5$. m-cu crossvein longer than basal section of vein M_4 . Mouth of subcostal cell longer than wing margin between R_1 and R_5 . Anal cell closed nearly at wing margin.

Genus *Prosolva* Hong: see p. 109.

Mostovski wrote: "It is not impossible that both *Mesosolva parva* Hong, 1983 and *Prosolva huabeiensis* Hong, 1983 belong to the same genus" (1996a: 329); "probably, the type species of the genus [= *Prosolva*] belongs to the genus *Mesosolva*" (1996b: 120). The mouth of subcostal cell and vein R_4 vary in length with species within *Mesosolva* (see Mostovski, 1996a). It is almost certain to us also that *Prosolva* is a junior synonym of *Mesosolva*, unless the characters given below are significant generically: mouth of subcostal cell distinctly longer than wing margin between R_1 and R_5 ; anal cell divergent apically (not convergent or not parallel-sided).

Prosolva(?) karataviensis Mostovski, 1996b, *Russian Entomol. J.*, 5: 120. Palearctic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 184 (= Mostovski, 1996b: fig. 14). Thorax 4 mm and wing 9.8 mm in length. This species differs from *Prosolva huabeiensis* and 8 known species of *Mesosolva* by having marginal cell closed (or nearly so) at wing margin.

Genus *Sharasargus* Mostovski, 1996b, *Russian Entomol. J.*, 5: 124. Type species: *Sharasargus ruptus* Mostovski, 1996, by original designation.

Similar to *Ovisargus* by having 4 (not 5) posterior cells, but differing from the latter in the following respects: anal cell open; discal cell more elongate; 2nd submarginal cell larger. In *Ovisargus gracilis*, anal cell petiolate, discal cell more robust, and 2nd submarginal cell small.

ruptus Mostovski, 1996b, *Russian Entomol. J.*, 5: 124. Palearctic: Mongolia (? Upper Jurassic) [Compression or impression].

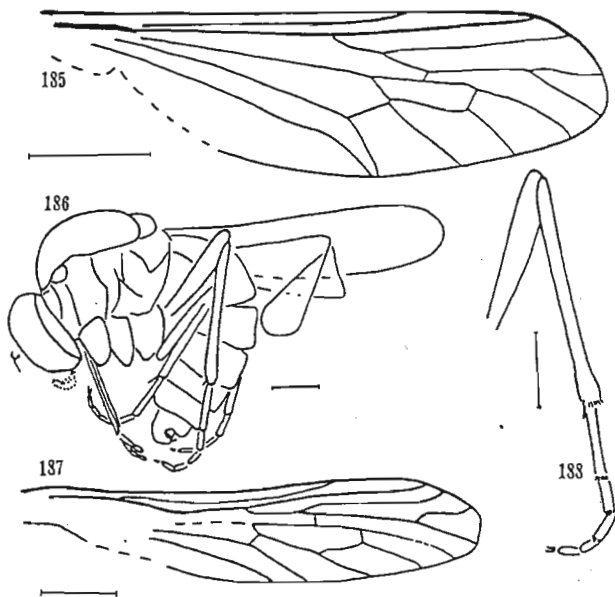
See fig. 185 (= Mostovski, 1996b: fig. 19). Wing 4.8 mm in length and 1.4 mm in width. Mouth of subcostal cell longer than wing margin between R_1 and R_5 ; basal section of vein R markedly long relative to that of Rs; marginal cell not narrowed apically and wide open; r-m crossvein situated about at middle of discal cell; vein M_3 absent; vein M_4 arising from 2nd basal cell and with basal section short; anal cell convergent apically but open; basal section of Rs about as long as that of vein $R_4 + R_5$. It appears that the alula is weakly developed.

Sharasargus(?) spiniger Mostovski, 1996b, *Russian Entomol. J.*, 5: 124. Palearctic: Kazakhstan (Upper Jurassic) [Compression or impression].

See figs 186–188 (= Mostovski, 1996b: figs 20–22). Body 8 mm and wing 7 mm in length (wing 1.5 mm in width). Wing differing from that of *Sharasargus ruptus* in the following respects: more elongate; vein M_4 arising from discal cell and section of discal cell

between m-cu and M_4 long; anal cell parallel-sided at apical portion and wide open; basal section of Rs much longer than that of vein $R_4 + R_5$.

Antennal flagellum totally bristle-like (if widened part just before arista represents pedicel); tibial spurs 0 : 1 : 1; male abdomen rounded apically.



Figs 185–188. — *Sharasargus* spp. (Archisargidae). 185, *S. ruptus* Mostovski; 186–188, *Sharasargus*(?) *spiniger* Mostovski (sex unknown) (188, hind leg). Scale bar = 1 mm. From Mostovski (1996b).

KEY 8: GENERA OF ARCHISARGIDAE

- 1 Vein R_{2+3} ending at vein R_1 far before wing margin 2
- Vein R_{2+3} ending at costa 3
- 2 Posterior cells 4 in number and vein M_3 absent: vein M_4 arising from apical part of discal cell; (figs 168–169) *Calosargus* (*Calosargus*) [*tatianae* and *niger*]
- Posterior cells 5 in number; vein M_3 complete and vein M_4 arising from basal part of discal cell; (fig. 170) *Calosargus* (*Pterosargus*) *thanasymus*
- 3 Posterior cells 4 in number 4
- Posterior cells 5 in number 6
- 4 Anal cell open; vein R_4 long and 2nd submarginal cell large relative to those of *Ovisargus*; discal cell more slender 5
- Anal cell petiolate; vein R_4 short and 2nd submarginal cell small; discal cell more robust; (figs 180–181) *Ovisargus gracilis*
- 5 Vein M_4 arising from 2nd basal cell; anal cell convergent apically; basal section of Rs about as long as that of vein $R_4 + R_5$; (fig. 185) *Sharasargus ruptus*
- Vein M_4 arising from discal cell; anal cell almost parallel-sided apically; basal section of Rs much longer than that of $R_4 + R_5$; (figs 186–188) ... *Sharasargus*(?) *spiniger*

- 6 Anal cell closed at or before wing margin 7
- Anal cell open 9
- 7 Marginal cell divergent or almost parallel-sided apically and wide open; vein Cu_1 long relative to that of *Archisargus* 8
- Marginal cell narrowed apically and closed or nearly so; vein Cu_1 markedly short; (figs 166–167) *Archisargus* (2 species)
- 8 Fourth posterior cell closed far before wing margin; vein R_5 about as long as 2nd section of vein $R_4 + R_5$; r-m crossvein situated at basal part of discal cell; basal section of Rs roughly $1/2$ as long as that of vein R; (fig. 182) *Parvisargus malus*
- Fourth posterior cell convergent apically but open; vein R_5 distinctly shorter than 2nd section of vein $R_4 + R_5$; r-m crossvein situated about at middle of discal cell; basal section of Rs roughly $1/4$ as long as that of vein R; (fig. 183) ... *Parvisargus peior*
- 9 Fourth posterior cell closed far before wing margin 10
- Fourth posterior cell divergent apically and wide open; (figs 7–9) *Archirhagio obscurus*
- 10 Marginal cell almost parallel-sided or divergent apically and always open 11
- Marginal cell narrowed apically and closed or nearly so; (fig. 184) *Prosolva*(?) *karataviensis*
- 11 Anal cell convergent or almost parallel-sided apically; (figs 11–14, 171–179) *Mesosolva* (8 species)
- Anal cell divergent apically (it is uncertain whether or not this character is significant generically); (figs 15–16) *Prosolva huabeiensis*

KEY 9: SPECIES OF MESOSOLVA (BASED ON MOSTOVSKI, 1996a)

- 1 Posterior section of 4th posterior cell not shorter than vein M_4 (= apical section of M_4) 2
- Posterior section of 4th posterior cell shorter than vein M_4 ; [vein R_5 shorter than 2nd section of $R_4 + R_5$; r-m crossvein situated at basal part of discal cell; base of discal cell situated opposite 1st fork of Rs; vein M_1 longer than anterior section (beyond r-m) of discal cell]; (fig. 175) *dolosa*
- 2 Vein M_1 as long (or nearly as long) as anterior section (beyond r-m) of discal cell 3
- Vein M_1 longer than anterior section (beyond r-m) of discal cell 6
- 3 Vein M_2 distinctly longer than distal posterior section of discal cell; r-m crossvein situated at basal part of discal cell; base of discal cell shifted distad from 1st fork of Rs 4
- Vein M_2 nearly as long as distal posterior section of discal cell; r-m crossvein situated at middle of discal cell; base of discal cell situated opposite 1st fork of Rs; (fig. 174) *angustocellulata*
- 4 Mouth of subcostal cell somewhat shorter than wing margin between R_1 and R_5 ; vein R_5 about as long as 2nd section of $R_4 + R_5$ 5
- Mouth of subcostal cell distinctly longer than wing margin between R_1 and R_5 ; vein R_5 distinctly shorter than 2nd section of $R_4 + R_5$; (fig. 177) *imperfecta*
- 5 r-m crossvein shifted distad from m-cu crossvein; discal cell more robust; (figs 11–14) *parva*
- r-m crossvein situated opposite m-cu crossvein; discal cell more elongate; (figs 178–179) *balyshvae*
- 6 Mouth of anal cell as long as or longer than m-cu crossvein; vein M_4 (= apical section of M_4) distinctly longer than distal section of 4th posterior cell 7
- Mouth of anal cell shorter than m-cu crossvein; vein M_4 (= apical section of M_4) as long as distal section of 4th posterior cell; [vein R_4 shorter than vein R_5 and than 2nd section of $R_4 + R_5$]; (fig. 173) *hennigi*
- 7 Vein R_5 distinctly shorter than 2nd section of $R_4 + R_5$; (fig. 176) *longivena*
- Vein R_5 about as long as 2nd section of $R_4 + R_5$; (figs 171–172) *rohdendorfi*

FAMILY ARCHOCYRTIDAE

Mostovski (1997) gave family status to Archocyrtinae Ussatchev, 1968. Ussatchev (1968) and Evenhuis (1994) put *Archocyrtus* in Acroceridae.

Archocyrtidae is similar to Eremochaetidae and Rhagionemestriidae in having vein $R_4 + R_5$ anastomosed with discal cell but is easily distinguished from the latter two by the absence of vein R_{2+3} . It would be more closely related phylogenetically to Acroceridae than to Eremochaetidae, if the lower calypter is much enlarged. Ussatchev (1968) wrote, "Tracheal trunk of squama [= calypter] apparent near base of right wing. Vein R_1 and part of $C + R_1$ are the thickest veins. The remaining veins are uniformly developed."

In Acroceridae, (1) abdomen robust, (2) C and R_1 markedly thickened, (3) vein R_{2+3} often evanescent, (4) antennal flagellum unsegmented, longer than scape + pedicel and often broad. All of the above characters are so in *Archocyrtus*. It is uncertain to us whether *Archocyrtus* represents an independent family or a subfamily of Acroceridae. In Table 1, it is treated traditionally as Acroceridae.

Genus *Archocyrtus* Ussatchev, 1968, *Ent. Obozr.*, 47: 622. Type species: *Archocyrtus gibbosus* Ussatchev, 1968, by original designation. *gibbosus* Ussatchev, 1968, *Ent. Obozr.*, 47: 622. Palearctic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 189 (= Ussatchev, 1968: fig. 5). Wing 2 mm and abdomen 3.1 mm in length. Vein R_{2+3} absent. Vein $R_4 + R_5$ arising from discal cell and forked. Posterior cells 4 in number. Vein M_3 absent and vein M_4 arising from discal cell. Mouth of subcostal cell large and much longer than wing margin between R_1 and R_5 . Marginal cell apparently closed at wing margin. Vein R_5 ending beyond wing apex. Fourth posterior cell large and divergent apically. [Anal cell not clearly seen.] Large lower calypter apparently present. Antennal flagellum unsegmented, longer than wide, longer than scape + pedicel, and not narrower than scape or pedicel. Abdomen robust. [Legs missing.]

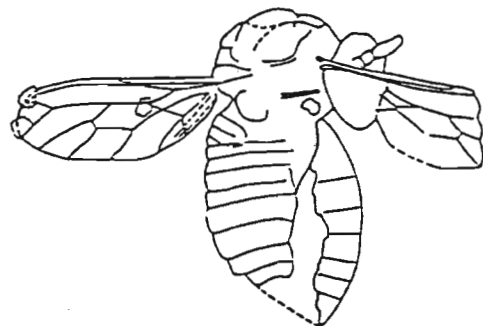


Fig. 189. — *Archocyrtus gibbosus* Ussatchev, ♀ (?) (Archocyrtidae). From Ussatchev (1968).

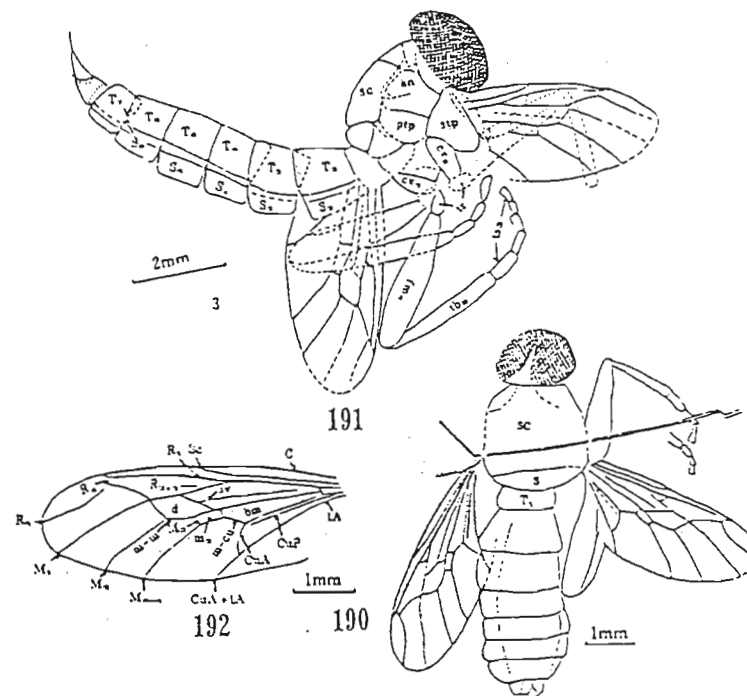
FAMILY EREMOCHAETIDAE

This family may easily be separated from the Archisargidae and Kovalevisargidae by having part of R veins anastomosed with discal cell and $r-m$ crossvein absent. It is distinguished from Archocyrtidae and Rhagionemestriidae as shown in the key 7. The presence or absence of $r-m$ crossvein may have no significance as a family character. If so, the Eremochaetidae would become a junior synonym of Archisargidae. There are three additional genera introduced below.

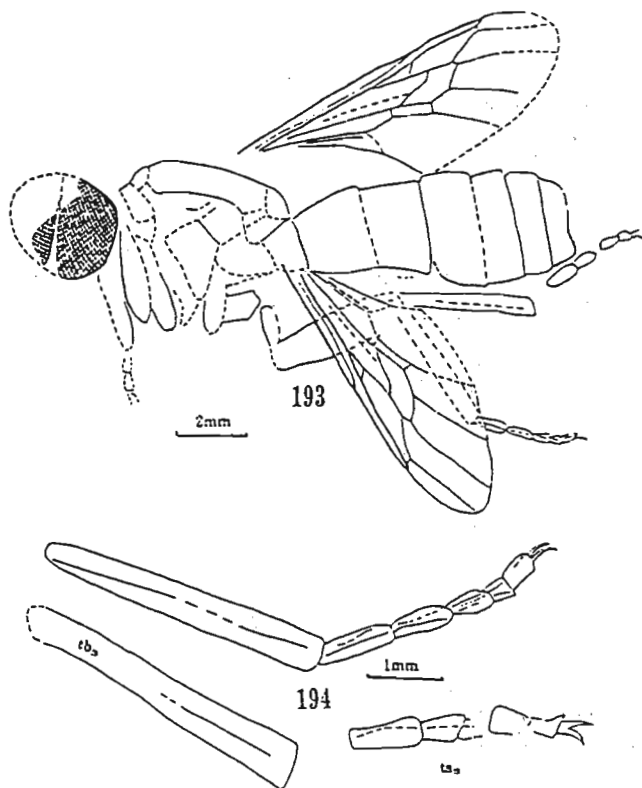
Genus *Alleremonomus* Ren & Guo, 1995, *Entomologia Sinica*, 2: 301.

Type species: *Alleremonomus xingi* Ren & Guo, 1995, by original designation.

Alleremonomus is peculiar by having vein R_4 ending on vein R_1 before wing margin. Apart from this character, it is similar to *Dissup*, *Eremochaetus* and *Pareremochaetus* where vein R_{2+3} ends on vein R_1 far before wing margin but is easily separated from them by having 2nd submarginal cell not triangular but rather elliptic in shape; discal cell and 4th posterior cell small and much shorter than each of veins M_1 and M_2 ; anal cell closed far before wing margin.



Figs 190–192. — *Alleremonomus xingi* Ren & Guo (Eremochaetidae). 190, Holotype (♂); 191, paratype (♀); 192, holotype (♂). From Ren & Guo (1995).



Figs 193–194. — *Alleremonomus liaoningensis* Ren & Guo (Eremochaetidae). 194, Hind tibiae and tarsi (“empodia unknown”). From Ren & Guo 1995.

Ren & Guo (1995: 301) wrote,

“It is interesting to note that the wing of the new genus has a spurious vein which is only found in existing species of Syrphidae of Aschiza. We suspect that ‘vena spuria’ is actually present in the specimen No. LB94001 (holotype of *Alleremonomus xingi*), [because it is] quite faint and not easily seen in the other materials (paratype of *A. xingi* and holotype of *A. liaoningensis*).

Ren and Guo (1995) described 2 new species of this genus from NE. China (Liaoning Province: Beipiao City) (Upper Jurassic): *xingi* (body [holotype] 7.7 mm and wing 4.5 mm in length); *liaoningensis* (body 16.5 mm and wing 10.2 mm in length). They wrote (p. 306), “[*A. liaoningensis*] differs from [*A. xingi*] ... by large body, longer cell M_3 [= 4th posterior cell] and shape of [discal cell].”

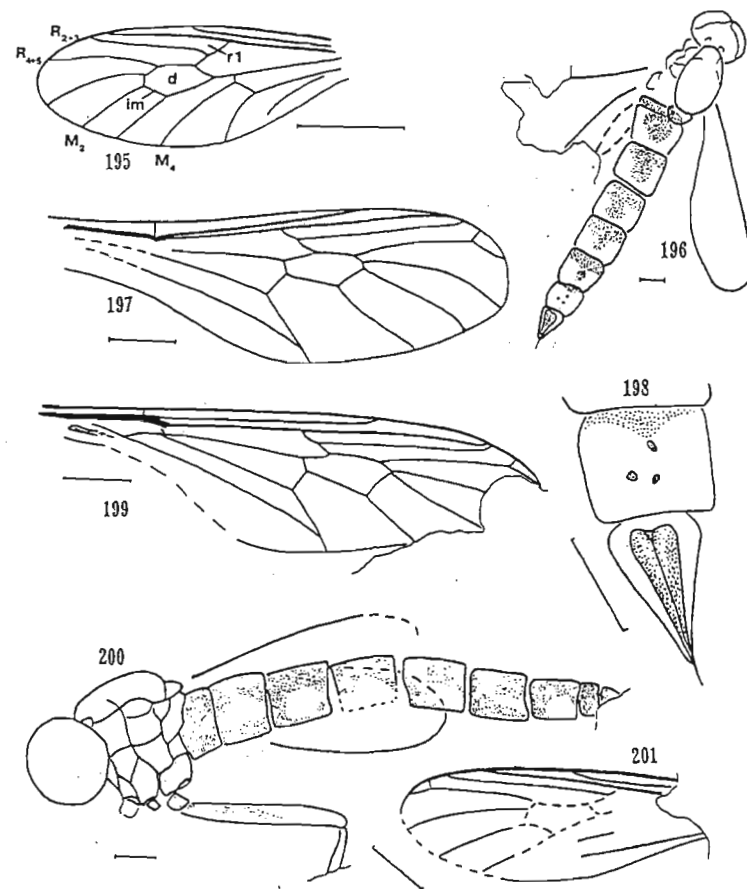
See figs 190–194 (= Ren & Guo, 1995: figs 2–4, 6–7).

Genus *Eremochaetomima* Mostovski, 1996, *Russian Entomol. J.*, 5: 118.

Type species: *Eremochaetomima incompleta* Mostovski, 1996, by original designation.

incompleta Mostovski, 1996, *Russian Entomol. J.*, 5: 118. Palearctic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 195 (= Mostovski, 1996b: fig. 1). Wing 3 mm in length. Vein $R_4 + R_5$ unforked (or vein R_4 absent). Anal cell wide open; vein A_1 probably incomplete or not reaching to wing margin. Mouth of subcostal cell not longer than wing margin between R_1 and R_2 ; vein R_{2+3} ending on costa and marginal cell open; vein R_5 (or R_{4+5}) ending before wing apex; vein M_4 arising from 2nd basal cell.



Figs 195–201. — Eremochaetidae. 195, *Eremochaetomima incompleta* Mostovski; 196–199, *Eremomukha (E.) isokotukha* Mostovski (196–198, holotype [♀]; 199, paratype); 200–201, *Eremomukha (E.) insidiosa* Mostovski, ♀. Scale bar = 1 mm. From Mostovski (1996b).

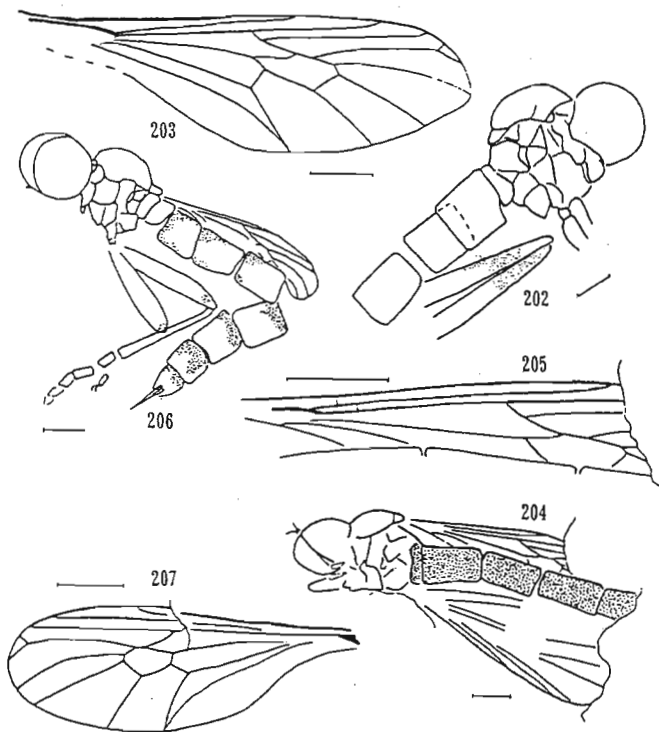
Genus *Eremomukha* Mostovski, 1996, *Russian Entomol. J.*, 5: 118. Type species: *Eremomukha tsokotukha* Mostovski, 1996, by original designation.

tsokotukha Mostovski, 1996, *Russian Entomol. J.*, 5: 118. Palaearctic: Mongolia (Lower Cretaceous) [Compression or impression].

See figs 196–199 (= Mostovski, 1996b: figs 2–5). Body (minus ovipositor) 14 mm and wing 7 mm in length (holotype), wing 7.3 mm in length (paratype). Posterior cells 4 in number and vein M_4 (arising from 2nd basal cell) absent. Anal cell petiolate. Vein R_4 shorter than vein R_5 . Mouth of marginal cell apparently narrowed apically but open. Needle-like ovipositor seen. For possible characters of *Eremomukha* (*Eremomukha*), see key 10 (couplet 2).

insidiosa Mostovski, 1996, *Russian Entomol. J.*, 5: 118. Palaearctic: Mongolia (Lower Cretaceous) [Compression or impression].

See figs 200–201 (= Mostovski, 1996b: figs 6–7). Body 14.5 mm and wing 7.5 mm in length. [Anal cell and discal cell not clearly seen]. Mouth of marginal cell not narrowed apically.



Figs 202–207. — Eremochaetidae. 202–205, *Eremomukha* (*Eremocreta*) *sorosi* Mostovski (202–203, holotype; 204–205, paratype); 206, *E. (Eremocreta) posita* Mostovski, ♀; 207, *E. (Eremocreta) addita* Mostovski. Scale bar = 1 mm. From Mostovski (1996b).

Subgenus *Eremomukha* (*Eremocreta*) Mostovski, 1996, *Russian Entomol. J.*, 5: 118. Type species: *Eremomukha (Eremocreta) sorosi* Mostovski, 1996, by original designation.

Mostovski (1996b: 118) described 3 new species of this subgenus from Siberia (Buryat Rep.) (Lower Cretaceous): *addita* (wing length 5.6 mm); *posita* (body 10.5 mm and wing 5.2 mm in length); *sorosi* (wing 6.3(?)–7.2 mm in length). See figs 202–207 (= Mostovski, 1996b: figs 9–13).

Mouth of marginal cell not narrowed apically. Anal cell petiolate or closed at wing margin. Ovipositor needle-like (seen in *posita*) and antennal flagellum totally bristle-like or at least apically (seen in *sorosi*). For possible characters of *Eremomukha* (*Eremocreta*), see key 10 (couplet 2).

KEY 10: GENERA OF EREMOCHAETIDAE

- 1 Posterior cells 4 in number or vein M_4 (arising from 2nd basal cell) absent; (anal cell petiolate; vein R_4 short and distinctly less than vein R_5) [Subfamily Eremomukhinae Mostovski, 1996] 2
- Posterior cells 5 in number or vein M_4 present [Subfamily Eremochaetinae Ussatchev, 1968] 3
- 2 (a) Basal section of $R_4 + R_5$ (= section between 1st submarginal and 1st basal cells) about as long as basal section of R_5 ; (b) section between discal and 1st basal cells shorter than that between discal and 1st submarginal cells; [the characters above may be not significant subgenerally]; (figs 196–201) *Eremomukha* (*Eremomukha*)
- (a) longer; (b) longer; (figs 202–207) *Eremomukha* (*Eremocreta*)
- 3 Vein R_{2+3} ending on vein R_1 far before wing margin 4
- Vein R_{2+3} ending at costa 7
- 4 Vein R_4 (if present) ending on costa; anal cell narrowly open (or vein A_1 incomplete) 5
- Vein R_4 ending on vein R_1 before wing margin; anal cell closed far before wing margin; (4th posterior cell closed far before wing margin as in *Dissup*; vein R_{2+3} arising from 1st basal cell as in *Eremochaetus* and *Pareremochaetus*); (figs 190–194) *Alleremonomus*
- 5 Vein R_{2+3} arising from 1st basal cell; 4th posterior cell wide open 6
- Vein R_{2+3} arising from discal cell; 4th posterior cell closed far before wing margin; (vein R_4 present; antennal flagellum totally bristle-like or at least apically); (figs 19–21) *Dissup*
- 6 Vein $R_4 + R_5$ forked or vein R_4 present; vein R_{2+3} long and ending near wing margin; vein A_1 complete; (fig. 25) *Eremochaetus*
- Vein $R_4 + R_5$ unforked or vein R_4 absent; vein R_{2+3} short and ending opposite apex of vein Sc ; vein A_1 incomplete; (antennal flagellum club-shaped and 6-segmented); (fig. 26) *Pareremochaetus*
- 7 Marginal cell closed at wing margin; vein A_1 probably complete and anal cell apparently convergent apically; (it is uncertain whether vein R_4 present or absent); (figs 22–24) *Eremochaetosoma*
- Marginal cell distinctly open; vein A_1 probably incomplete and anal cell apparently divergent apically; (vein R_{2+3} arising from 1st basal cell; vein R_4 absent; vein R_5 ending before wing apex); (fig. 195) *Eremochaetomima*

FAMILY KOVALEVISARGIDAE

This family may be separated from the Archisargidae and Sino-nemestrinidae by having:

vein $R_4 + R_5$ unforked (or vein R_4 absent) and vein M_1 arising far before apex of discal cell.

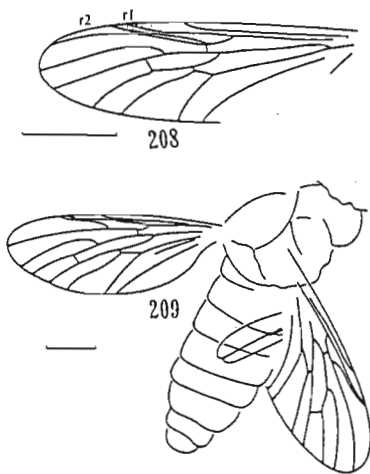
Subcostal cell divergent apically and wide open, but its mouth distinctly shorter than wing margin between R_1 and R_2 . Marginal cell widened at base and narrowly open apically. Mouth of submarginal cell very wide and much longer than that of 1st posterior cell. Posterior cells 5 in number and vein M_4 arising from 2nd basal cell. Fourth posterior cell divergent apically. Anal cell wide open and almost parallel-sided apically. Abdomen may be more robust than in Archisargidae but hind leg is apparently markedly long as in the latter (seen in *Kerosargus argus*).

Genus *Kovalevisargus* Mostovski, 1997, *Paleontol. J.*, 1997 (No. 1): 76.

Type species: *Kovalevisargus clarigenus* Mostovski, 1997, by original designation.

clarigenus Mostovski, 1997, *Paleontol. J.*, 1997 (No. 1): 76. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 208 (= Mostovski, 1997: fig. 3a). Wing 6.6 mm in length. Vein R_{2+3} arising from r-m crossvein. Vein R_5 (or R_{4+5}) ending before wing apex. Mouth of anal cell longer than m-cu crossvein. Discal cell more robust than in *Kerosargus argus* and veins M_2 and M_3 longer than discal cell.



Figs 208–209. — Kovalevisargidae. 208, *Kovalevisargus clarigenus* Mostovski; 209, *Kerosargus argus* Mostovski. From Mostovski (1997).

Genus *Kerosargus* Mostovski, 1997, *Paleontol. J.*, 1997 (No. 1): 76. Type species: *Kerosargus argus* Mostovski, 1997, by original designation. *argus* Mostovski, 1997, *Paleontol. J.*, 1997 (No. 1): 76. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 209 (= Mostovski, 1997: fig. 3b). Body 11 mm and wing 9 mm in length. Vein R_{2+3} arising far beyond r-m crossvein. Vein R_5 (or R_{4+5}) ending at wing apex. Mouth of anal cell shorter than m-cu crossvein. Discal cell more slender than in *Kovalevisargus clarigenus* and veins M_2 and M_3 shorter than discal cell. Abdomen rounded apically.

FAMILY NEMESTRINIDAE

No extensive *personal* study has been made on Nemestrinidae, but we are able to refer to Bernardi (1972, 1973a,b, 1975) on the genera and wing venation of this family. There is one definite synapomorphic character state throughout the known genera of this family: veins M_2 and M_4 diagonal and 4th posterior cell closed far before wing margin. It is also seen in Mydidae and Apioceridae where *marginal cell* is closed far before wing margin. However, *marginal cell* is wide open in Nemestrinidae and closed at wing margin in Sino-nemestrinidae (where vein M_4 is not diagonal). Based on Bernardi (1973b: figs 14–38), the following are added to the features of Nemestrinidae:

mouth of subcostal cell wide open, although its length varies with taxon; apical portion of 1st basal cell usually long, narrow and pointed; vein $R_4 + R_5$ forked or sometimes unforked; anal cell usually open; vein $R_4 + R_5$ arises either from 1st basal cell (r-m crossvein present) or from discal cell (r-m crossvein absent); alula absent, ill-developed or distinct.

Bernardi (1972: 49) wrote,

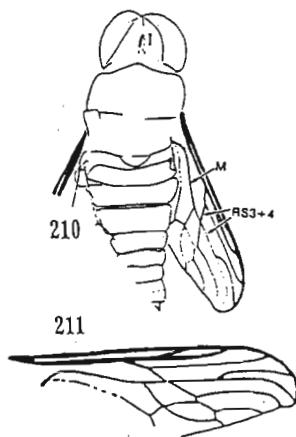
“The most important point in relation to the removal of *Exeretonevra* from the Nemestrinidae is the role played by the branches of media, especially in the formation of the *diagonal vein*, which is the most conspicuous character of the nemestrinid venation. In all nemestrinids the end of the *diagonal vein* is formed by M_{3+4} , except where this portion is lost (*Stenopteromyia*, *Fallenia* and some *Neorhynchocephalus*) and does not reach the hind margin of the wing. In these cases, however, there is no problem of interpretation. M_{3+4} is an important element of the *diagonal* even in the most specialized genera in respect to wing venation, like *Nycterimymia* and *Nycterimorpha*, and even in the known Jurassic fossils (Rohdendorf 1968). The condition found in *Exeretonevra* is quite different from that found in the Nemestrinidae. That is why I said its resemblance to the nemestrinid pattern is only superficial.”

Genus *Archinemestrius* Rohdendorf, 1968, *Jurassic insects of the Karatau* (Akademia Nauka, Moscow), p. 181. Type species: *Archinemestrius karatavicus* Rohdendorf, 1968, by original designation. *karatavicus* Rohdendorf, 1968: 181. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See Figs 210–211. *Archinemestrius karatavicus* is peculiar among Nemestrinidae in the following respects:

vein R_5 ending around wing tip but curved downward at apical portion; veins M_1 and M_2 ending at hind margin of wing.

Veins C and R_1 markedly thickened. Mouth of subcostal, marginal, 1st and 2nd submarginal cells relatively long respectively. First basal cell not longer than 2nd basal cell. Vein $R_4 + R_5$ arising from discal cell at or near apex of 1st basal cell. Veins M_1 , M_2 , and M_4 almost diagonal. Vein M_4 ending at M_3 and 4th posterior cell closed far before wing margin. [Postero-proximal part of wing unknown]. Abdomen broad but tapering apically.



Figs 210–211. — *Archinemestrius karatavicus* Rohdendorf (Nemestrinidae). 210, from Carpenter (1992); 211, from Bernardi (1973b); both originally from Rohdendorf (1968).

It is stressed in the original description that 'phragma' (= basal section of 1st basal cell or crossvein between base of wing and 1st basal cell) is absent.

Rohdendorf (1968) wrote,

"Head short, apparently lacking the long proboscis. Eyes holoptic (male?). There are three very small ocelli. Antennae thin and short, composed of not less than four homonomous joints. Thorax somewhat broader than the head." (translated by Bernardi, 1973b: 237–238).

Rohdendorf (1968) placed *Archinemestrius* in Archinemestriinae Rohdendorf, 1968.

Genus *Eohirmoneura* Rohdendorf, 1968, *Jurassic insects of the Karatau* (Academia Nauka, Moscow), p. 187. Type species: *Eohirmoneura carpenteri* Rohdendorf, 1968, by original designation. *carpenteri* Rohdendorf, 1968: 188. Palaeartic: Kazakhstan (Upper Jurassic) [Compression or impression].

See figs 212–213. *Eohirmoneura carpenteri* is characterized in the following respects:

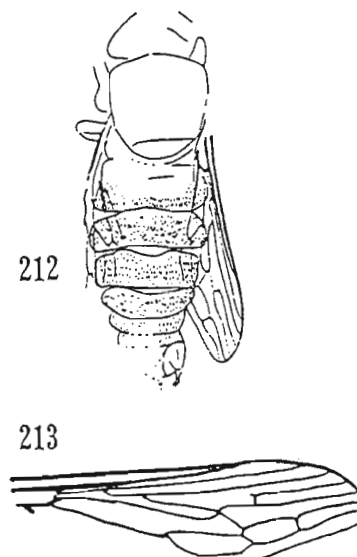
(1) vein M_{3+4} (reaching to wing margin) absent; (2) 2nd posterior cell with 1 complete crossvein around middle; (3) 1st submarginal cell with 1 incomplete crossvein near base of vein R_4 .

The presence or absence of (2) and (3) above may vary with species within *Hirmoneura*. If (1) is overlooked or lost accidentally, *Eohirmoneura* would be almost identical with *Hirmoneura* Meigen, 1820 where *H. willistoni* (Cockerell, 1910) is known from the USA (Oligocene). However, in *Eohirmoneura* vein Sc may be shorter relative

to that of *Hirmoneura* and 'phragma' (= basal section of 1st basal cell or crossvein between base of wing and 1st basal cell) may be not oblique but vertical.

Veins C and Sc apparently thickened. Abdomen broad but tapering apically.

Eohirmoneura belongs to Hirmoneurinae.



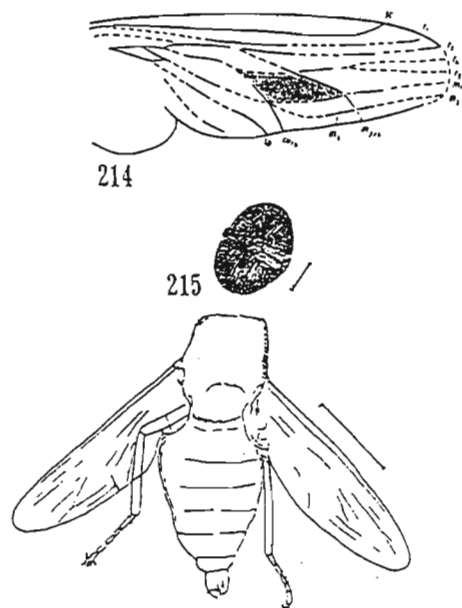
Figs 212–213. — *Eohirmoneura carpenteri* Rohdendorf (Nemestrinidae). [It has been judged that discal cell is present and its basal section is overlooked in Fig. 213.] 212, From Carpenter (1992); 213, from Bernardi (1973b); both originally from Rohdendorf (1968).

Genus *Prohirmoneura* Handlirsch, 1906, *Die fossilen Insekten und die Phylogenie der rezenten Formen (Ein Handbuch für Paläontologen und Zoologen*. Engelmann, Leipzig). p. 633. Type species: *Prohirmoneura jurassica* Handlirsch, 1906, by monotypy.

jurassica Handlirsch, 1906: 633. Palaeartic: Germany (Upper Jurassic) [Compression or impression].

See figs 214–215 (= Handlirsch, 1906: figs 11–12). Head is 5.2 mm in width, thorax + abdomen 17 mm and wing about 13 mm in length. Handlirsch (1906: 633) wrote,

"Eine hochinteressante Form mit grossem Kopf, dessen mächtig entwickelte Facettenaugen auf der Stirne zusammenstossen, mit einem kurzen nach den gerichteten Rüssel, etwas gedrungenem Körper und kräftigen Beinen. Die schlanken Flügel lassen das Geäder wohl nur undeutlich erkennen doch sieht man aus den wenigen Aderresten ganz deutlich, dass es jenem der rezenten Nemestriniden ähnlich war. Der Anallappen ist gross."



Figs 214–215. — *Prohirmoneura jurassica* Handlirsch (Nemestrinidae). 214, From Hennig (1954) [originally from Handlirsch (1906)]; 215, from Handlirsch (1906).

Bequaert & Carpenter (1936) and Ussatchev (1968) placed *Prohirmoneura* near living *Hirmoneura* Meigen, 1820 [where *H. willistoni* (Cockerell, 1910) is known from USA (Oligocene)] belonging to Hirmoneurinae, but Bernardi (1973b: 282) wrote, "this fossil is very badly preserved and its position in the family is impossible to assess. It may be more probably a Hirmoneurinae, but there is no sound basis for this placement."

If the presence of enlarged lower calypter is true, the position of *Prohirmoneura* would become quite problematic.

Genus *Protonemestrius* Rohdendorf, 1968, *Jurassic insects of the Karatau* (Akademia Nauka, Moscow), p. 182. Type species: *Protonemestrius martynovi* Rohdendorf, 1968, by original designation.

Protonemestrius is similar to *Archinemestrius* by having no 'phragma', having C and R₁ markedly thickened, and having Sc short, but different from the latter in the following respects:

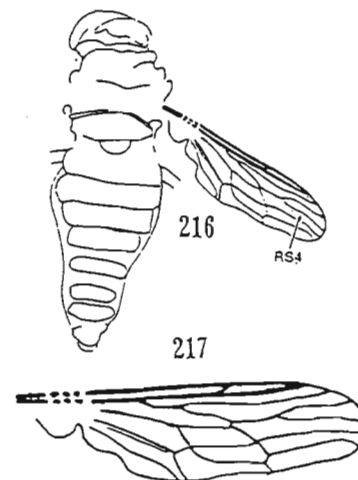
r-m crossvein distinct; vein R₅ not curved downward at apical portion; vein M₂ relatively long; 1st basal cell longer than 2nd basal cell.

It is similar in wing venation to *Prosoeca* Schiner, 1867 (= *Palembolus* Scudder, 1878) [where *P. florigera* Scudder, 1878 from USA (Oligocene) is known], but different from the latter in the following points:

presence of 3 characters common to *Archinemestrius* mentioned above; vein M₂ curved downward at apical portion and ending distinctly beyond wing apex; discal and 4th posterior cells more robust. In *Prosoeca*, vein M₂ straight, running upwards, and ending at wing apex; discal and 4th posterior cells more elongate.

Rohdendorf (1968) wrote, "Head slightly prolonged, with prominent proboscis. Thorax not particularly broad. Legs with slightly broadened femora and narrow tibiae and tarsi; hind tibiae with short spurs, tarsi with bristles" (translated by Bernardi, 1973b: 238). Alula well developed; abdomen broad and tapering apically (see fig. 211).

Rohdendorf (1968) placed *Protonemestrius* in Archinemestriinae Rohdendorf, 1968, but it is uncertain to us whether the identity of this genus is Archinemestriinae or Nemestrininae (in which *Prosoeca* belongs).



Figs 216–217. — *Protonemestrius martynovi* Rohdendorf (Nemestrinidae). 216, from Carpenter (1992); 217, from Bernardi (1973b); both originally from Rohdendorf (1968).

Rohdendorf (1968) described the following 4 new species from Kazakhstan (Upper Jurassic) [Compression or impression]: *bequaerti*; *handlirschi*; *longinasus*; *martynovi*. See figs 216–217 and Rohdendorf (1968: figs 2–5).

KEY 11: MESOZOIC GENERA AND SPECIES OF NEMESTRINIDAE

- 1 Vein Sc short and ending opposite at or before apex of discal cell; enlarged lower calypter probably absent 2
- Vein Sc long and ending opposite beyond apex of discal cell; enlarged lower calypter apparently present; [wing venation not clear but probably similar to that of *Hirmoneura*]; (figs 214–215) *Prohirmoneura jurassica*
- 2 Vein M₂ ending beyond wing apex; vein M₃₊₄ present (or vein M₃ reaching to wing margin); 2nd posterior cell without crossvein; 'phragma' [= crossvein between base of wing and 1st basal cell] absent 3
- Vein M₂ ending at wing apex; vein M₃₊₄ absent (or vein M₃ not reaching to wing margin) (if not overlooked); 2nd posterior cell with crossvein at middle; 'phragma' present; (figs 212–213) *Eohirmoneura carpenteri*

- 3 Veins R_5 and M_1 curved downwards at distal portion; vein $R_4 + R_5$ arising from discal cell; vein M_2 shorter than vein R_4 ; (figs 210–211) *Archinemestrius karatavicus*
 — Veins R_5 and M_1 not curved downwards; vein $R_4 + R_5$ arising from 1st basal cell (or r-m crossvein present); vein M_2 longer than vein R_4 ; (figs 216–217)
 *Protonemestrius* (4 species)

FAMILY RHAGIONEMESTRIIDAE, stat. n.

Rhagionemestriinae Ussatchev, 1968. Type genus: *Rhagionemestrius* Ussatchev, 1968.

This family falls in lower branch of couplet 3 in the original key 4 (p. 100), that is, Eremochaetidae, but is distinguished from the latter by having costa + vein R_1 markedly thickened and ending at apex of vein R_5 beyond wing tip (see also key 7 [couplet 5¹]).

Ussatchev (1968) wrote,

" R_1 extends practically to R_5 where it coalesces with C; it may therefore be considered that the veins R_{2+3} and R_4 join R_1 rather than C. . . . C extends the length of the wing. C, Sc and R [= R_1] are the thickest veins. The area of the wing between C and R_1 is darkened and strongly sclerotized."

Bernardi (1973a) wrote,

"The most interesting feature of the venation of *Rhagionemestrius* is the course taken by R_1 . This vein runs besides C along the whole wing apex to approximately the level of R_5 , where it fuses with C, so that R_2 and R_4 end in R_1 and not in C. To my knowledge, cases of a similar course of R_1 occur only in some *Pelecorhynchus* [Pelecorhynchidae of Tabanoidea], although in this genus R_1 is not so strongly directed backwards."

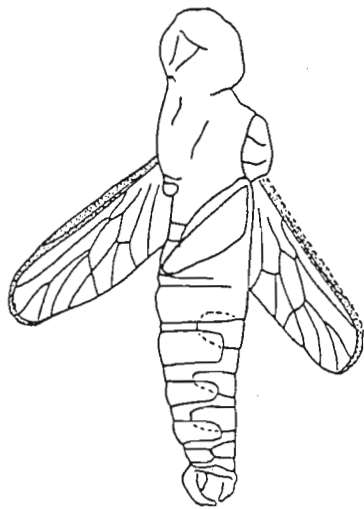


Fig. 218. — *Rhagionemestrius rapidus* Ussatchev, ♂ (Rhagionemestriidae). From Bernardi (1973a); originally from Ussatchev (1968).

Genus *Rhagionemestrius* Ussatchev, 1968, *Entomol. Obozr.*, 47: 621.

Type species: *Rhagionemestrius rapidus* Ussatchev, 1968, by original designation.

rapidus Ussatchev, 1968: 621. Palaearctic: Kazakhstan (Upper Jurassic) [Compression or impression].

See fig. 218 (= Ussatchev, 1968: fig. 4). Thorax 2.3 mm, abdomen 5.3 mm and wing 3.8 mm in length. Ussatchev (1968) wrote, "Eyes large, occupying almost the entire surface of the head. Ocelli present. Face convex along mouth margin. . . there is . . . a noticeably thickened hind femur . . . The abdomen is widest in the area of the 3rd segment. The basimeres of the hypopygium are medially greatly distended; the distimeres are recurved and basally narrowed." Marginal cell judged to be closed at wing margin; vein M_3 arising at base of M_2 and 3rd posterior cell pointed basally; vein M_4 arising from 2nd posterior cell; both 4th posterior cell and anal cell wide open; [presence or absence of alula unknown; lower calypter presumably not enlarged].

Position of *Rhagionemestrius*

Bernardi (1973a) wrote,

"It [= *Rhagionemestrius*] is undoubtedly not a nemestrinid. . . The above mentioned characters are not sufficient to include *Rhagionemestrius* among the Nemestrinidae. They rather show that the genus probably belongs to a very distinct group, which might be better considered a different family. It is not even more closely related to the Nemestrinidae than to other families. . . If *Rhagionemestrius* is considered to be near the ancestral stock of the Nemestrinidae, it might as well be considered a putative ancestor for other families widely separated from the Nemestrinidae. Based on the elongate R_1 , for instance, why not consider *Rhagionemestrius* a primitive Pelecorhynchidae? . . . Summing up, in my opinion, there is no reason to consider *Rhagionemestrius* a nemestrinid, and, until conclusive evidence is available, I think it better to ascribe it to some other family."

However, *Rhagionemestrius* differs considerably from the genera of Pelecorhynchidae, that is, *Glutops*, *Pseudoerinna* (= *Bequaertomyia*), and *Pelecorhynchus* (see e.g., Mackerras & Fuller, 1942; Nagatomi & Saigusa, 1970; Teskey, 1981) in general appearance and wing venation. The vein $R_4 + R_5$ arising from discal cell is seen in Eremochaetidae, Rhagionemestriidae, Archocyrtidae, some Nemestrinidae and some Acroceridae. It is also seen exceptionally in *Exeretonevra* (Exeretonevridae of Xylophagoidea). If it is seen more often or almost exclusively in Nemestrinoidea, *Rhagionemestrius* would fall in this superfamily in higher probability or almost inevitably.

SINONEMESTRIIDAE, Fam. n.

Type genus: *Sinonemestrius* Hong & Wang, 1990.

This family is similar to Nemestrinidae by having veins M_1 and M_2 diagonal but is easily separated from the latter in the following respects:

vein M_4 running downwards and 4th posterior cell not closed far before wing margin but narrowly open or nearly closed at wing margin; mouth of subcostal cell apparently short; marginal cell closed at wing margin. It is peculiar in having mouth of 3rd posterior cell conspicuously long and 2nd posterior cell narrowed apically and much shorter in mouth length than 3rd posterior cell.

Genus *Sinonemestrius* Hong & Wang, 1990, *The stratigraphy and palaeontology of Laiyang Basin, Shandong Province* (Shandong Bureau of Geology and Mineral Resources, China), p. 149.

Type species: *Sinonemestrius tuanwangensis* Hong & Wang, 1990, by original designation.

tuanwangensis Hong & Wang, 1990: 150. China (Upper Jurassic) [Compression or impression].

See fig. 219 (= Hong & Wang, 1990: fig. 150). Wing 13 mm in length. Only wing is known. The characters mentioned in the family diagnosis are omitted here. 'r-m' in fig. 219 is not r-m but proximal section of 1st basal cell (= 'phragma' or 'anterior branch of media').

Vein R_5 [= Rs_1] and vein M_1 end at or very near wing tip. Apical portion of 1st basal cell long and narrow as in usual Nemestrinidae. r-m crossvein [= rs-m] arising beyond middle of discal cell. Mouth of 1st submarginal cell much longer than that of 2nd submarginal cell. First posterior cell narrowed apically. Vein M_3 short. Vein M_4 arising from 2nd basal cell. Both 4th posterior cell and anal cell convergent apically and narrowly open.

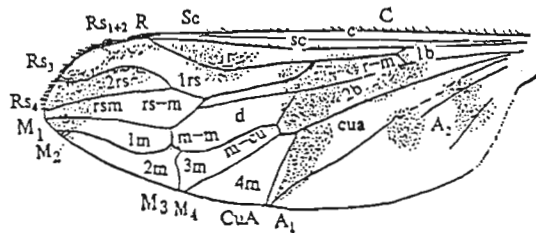


Fig. 219. — *Sinonemestrius tuanwangensis* Hong & Wang (Sinonemestriidae). From Hong & Wang (1990).

Position of *Sinonemestrius*

Only the wing is known and determination of the phylogenetic position is difficult. *Sinonemestrius* is placed here provisionally in Nemestrinoidea on the basis of only one character: veins M_1 and M_2 are diagonal. It is somewhat similar in wing venation to *Heterostomus* (Heterostomidae), *Exeretonevra* (Exeretonevridae) and *Odontosabula* (Coenomyiidae) belonging to Xylophagoidea (see, e.g. Nagatomi & Saigusa, 1970; Bernardi, 1972; Nagatomi, 1985), but differs from them in the following respects: 2nd posterior cell narrowed apically and its mouth much shorter than that of 3rd posterior cell.

For differences of wing venation between Nemestrinidae and Mydidae + Apioceridae, see notes under Nemestrinidae.

Judging from the possible age of the respective superfamily, it is more probable that *Sinonemestrius* falls in Nemestrinoidea rather than in Asiloidea, unless *Sinonemestrius* belongs to Xylophagoidea.

ANTENNAL FLAGELLUM, TIBIAL SPURS, EMPIDIUM, NEEDLE-LIKE OVIPOSITOR, AND SLENDER OR ROBUST ABDOMEN IN NEMESTRINOIDEA

1

These characters are seen in the extinct Mesozoic taxa as below.

1. Antennal flagellum.

(a) Totally bristle-like or at least apically. Archisargidae: *Archirhagio obscurus* (fig. 8); *Calosargus tatarianae* (fig. 168); *Mesosolva parva* (figs 11–12); *Sharasargus(?) spiniger* (fig. 186). Eremochaetidae: *Dissup irae* (fig. 21); *Eremochaetosoma mongolicum* (fig. 24); *Eremomukha (Eremocreta) sorosi* (fig. 199).

(b) Club-shaped and 6-segmented. Eremochaetidae: *Pareremochaetus minor* (fig. 26).

(c) Unsegmented, longer than wide, longer than scape + pedicel and not narrower than scape or pedicel: Archocyrtidae: *Archocyrtus gibbosus* (fig. 189).

(d) "Antennae thin and short, composed of not less than four homonomous joints" (Rohdendorf, 1968): Nemestrinidae: *Archinemestrius karatavicus* (fig. 210).

2. Tibial spurs. Archisargidae: *Sharasargus(?) spiniger*: 0 : 1 : 1 (figs 186, 188); "Fore tibiae without spurs but with nimbus of short bristles apically, middle ones with one spur and short apical bristles, hind tibiae thickened apically with one spur and short bristles": (Mostovski, 1996b: 124).

Nemestrinidae: *Protonemestrius martynovi*: "hind tibiae with short spurs" (Rohdendorf, 1968).

3. Empodium. Pulvilliform or pad-like. Archisargidae: *Archirhagio obscurus* (fig. 7). Eremochaetidae: *Pareremochaetus minor* (fig. 26).

Archisargidae: *Sharasargus(?) spiniger* (fig. 188): "It is difficult to say whether representatives of this species had empodium well developed or bristle-like" (Mostovski, 1996b: 124).

4. Needle-like ovipositor. Archisargidae: *Mesosolva balyshvaeae* (fig. 179); *Mesosolva parva* (figs 11, 13); *Ovisargus gracilis* (fig. 180). Eremochaetidae: *Alleremonomus xingi* (fig. 191); *Eremochaetosoma mongolicum* (fig. 22); *Eremomukha (Eremomukha) tsokotukha* (figs 196, 198); *Eremomukha (Eremocreta) posita* (fig. 206).

5a. Slender abdomen. Archisargidae: 6 genera and 6 species. Eremochaetidae: 5 genera and 8 species. Abdomen of *Sharasargus(?) spiniger* (fig. 186) (Archisargidae) may be somewhat robust but apparently falls in the category of slender abdomen.

5b. Somewhat robust abdomen. Kovalevisargidae: *Kerosargus argus* (fig. 209). Rhagionemestriidae: *Rhagionemestrius rapidus* (fig. 218).

5c. Abdomen broad and tapering apically. Nemestrinidae: *Archinemestrius karatavicus* (fig. 210); *Eohirmoneura carpenteri* (fig. 212); *Prohirmoneura jurassica* (fig. 215); *Protonemestrius martynovi* (fig. 217).

5d. Robust abdomen. Archocyrtidae: *Archocyrtus gibbosus* (fig. 189).

2

Concerning living Nemestrinidae and Acroceridae no extensive personal study has been made, but some comments are given below.

1. Antennal flagellum. Nemestrinidae: with 4 or sometimes 0–3 segments, and with base widened but sometimes not. Thus in some taxa, it is unsegmented and with base not so widened. See Bernardi (1973b: figs 1–13).

Acroceridae: always unsegmented, wider than, as wide as, or often much narrower than scape or pedicel.

Remarks. The shape of flagellum in some living taxa of Nemestrinidae and Acroceridae is reminiscent of that of Archisargidae and most Eremochaetidae whose flagellum would be bristle-like totally (if widened part before arista represents pedicel). The flagellum of *Archocyrtus gibbosus* (Archocyrtidae) may be similar to that of some Acroceridae. However, it must be noted that flagellum of *Pareremochaetus minor* (Eremochaetidae) is club-shaped and 6-segmented.

2. *Tibial spurs*. Nemestrinidae: "Tibial spurs lost" (after Woodley, 1989: 1383).

Acroceridae: "[tibia on each leg] sometimes produced into one or two apical spurs (Panopinae, fig. 37)" (after Schlinger, 1981: 577). However, this spur is probably not homologous with that of Xylophagoidea and Tabanoidea.

Remarks. Tibial spur formula is 0 : 1 : 1 in *Sharasargus*(?) *spiniger* (Archisargidae). "Hind tibiae with short spurs" (Rohdendorf, 1968) in *Protonemestrius martynovi* (extinct Mesozoic Nemestrinidae).

3. *Empodium*. Nemestrinidae and Acroceridae: pulvilliform or pad-like. Schlinger (1981: 577) wrote as to Acroceridae, "empodium developed pulvilliform (fig. 36); empodium on each leg much reduced in several genera, or pulvilli and empodium lacking entirely (*Camposella* Cole, Neotropical)."

Remarks. The presence of pulvilliform empodium is confirmed in 1 species of Archisargidae and 1 species of Eremochaetidae.

4. *Ovipositor* (including female cerci). Nemestrinidae: Bernardi (1973b: 218-219) wrote, "There are two types of ovipositor. Type 1: telescope-shaped, with many retractile segments and terminal valvulae short. Found in Hirmoneurinae, Nemestrininae and Cyclopsideinae. Type 2: sabre-shaped, with two extremely long and slender valvulae. Found in Trichopsideinae and Atriadopsinae."

Acroceridae: "Female terminalia (fig. 38) usually simple, consisting of enlarged cerci and a cup-shaped, scalloped, or trilobate sternite 8" (after Schlinger, 1981: 580).

Remarks. The presence of needle-like ovipositor is confirmed in Archisargidae (2 genera and 3 species) and Eremochaetidae (3 genera and 4 species).

5. *Thickness of abdomen*. Nemestrinidae: "Abdomen usually as wide as or wider than thorax, widest near middle, ..." (after Teskey, 1981: 586).

Acroceridae: "Abdomen globose, globose-elongate, or narrow and tapering or parallel-sided" (after Schlinger, 1981: 575).

Remarks. The presence of slender abdomen is confirmed in 7 genera (and 7 species) of Archisargidae and 6 genera (and 8 species) of Eremochaetidae. The abdomen is somewhat robust in *Kerosargus argus* (Kovalevisargidae) and markedly robust in *Archocyrtus gibbosus* (Archocyrtidae). In *Nycterimyia tenestro-inornata* (♂) (living Nemestrinidae), the abdomen is wider and shorter than that of Archisargidae and Eremochaetidae but widest at segment 5 or has segments 1-5 roughly parallel-sided like the latter 2 families (see Nagatomi, 1978: fig. 1c).

Possible tree of Nemestrinoidea constructed on wing

The tree is proposed as fig. 220, based on possible apomorphy (square mark) and plesiomorphy (circle mark).

1. Costa and vein R_1 markedly thickened at anterior distal portion (apomorphic) / not markedly thickened (plesiomorphic).
2. Veins M_1 and M_2 diagonal, or running upward or toward anterior margin of wing (apomorphic) / running downward or toward posterior margin of wing (plesiomorphic).
3. Vein M_1 arising far before apex of discal cell which is markedly slender; vein R_{4+5} unforked (apomorphic) / arising from at or near apex of discal cell which is more robust; forked but exceptionally unforked secondarily (plesiomorphic).
4. Part of R veins anastomosed with discal cell and r-m crossvein absent (apomorphic) / independent of discal cell and r-m crossvein present (plesiomorphic).
5. Vein M_4 diagonal and 4th posterior cell closed far before wing margin (apomorphic) / running downward and 4th posterior cell narrowly open or nearly closed (plesiomorphic).
6. Either (a) when all veins and all cells complete, one (sometimes two) additional cell present just before discal cell or one (or two) crossvein (besides r-m crossvein) present between 1st submarginal cell and 2nd posterior cell or (b) some veins (R_{2+3} and several M veins) evanescent and eventually venation becoming like that of Phoridae (apomorphic) / all veins and all cells complete and additional cell or crossvein absent (plesiomorphic).

7. Lower calypter enlarged (apomorphic) / not (plesiomorphic).

8. When vein $R_4 + R_5$ arises from discal cell, the number of M veins is 1 or 2 (apomorphic) / vein $R_4 + R_5$ arising from discal cell and 3 M veins complete (plesiomorphic).

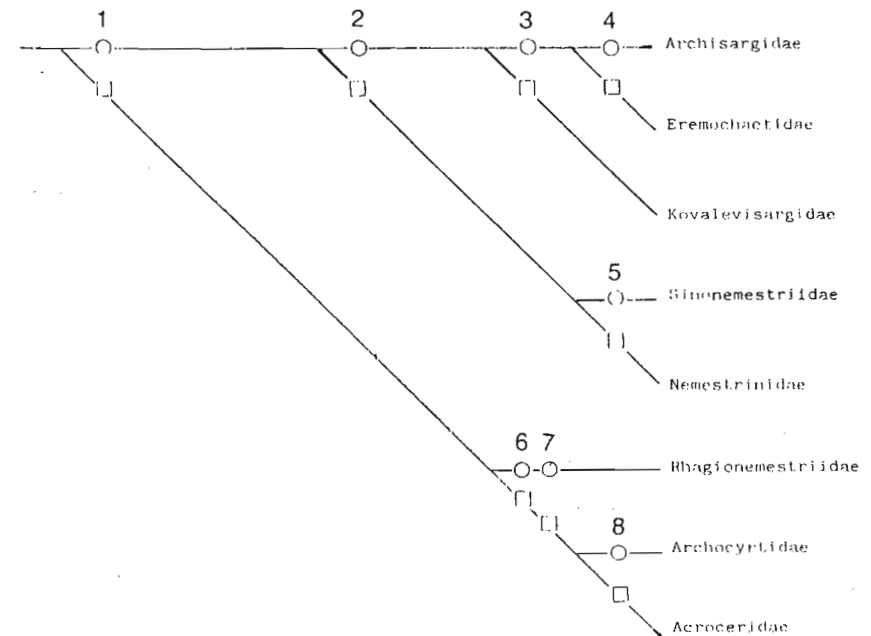


Fig. 220. — Possible tree of Nemestrinoidea constructed on wing.

Evaluations must be made on the character states above.

1: markedly thickened C and R_1 is more widespread in Acroceridae etc. than in Nemestrinidae etc. where it is seen sporadically and perhaps developed secondarily. However, the degree of thickness is gradual, no clear-cut distinction may be present between them, and several Mesozoic genera of Nemestrinidae (= *Archinemestrius*, *Eohirmonaura*, and *Protonemestrius*) have C and R_1 markedly thickened. The parallel development may be easy in markedly thickened C and R_1 . It is not necessarily certain whether the identity of Rhagionemestriidae is Acroceridae etc. or Nemestrinidae etc.

3: maybe not clear-cut.

4: maybe not significant as family diagnosis.

6: it is less probable that (a) is the ground plan of Acroceridae, that is, (b) is always derived directly from (a) within Acroceridae.

7: it is presumed that lower calypter is not enlarged in Rhagionemestriidae.

8: no extensive *personal* study has been made on Acroceridae by us.

Thus, the characters used in (1), (3), (4), (6), (7) and (8) may have little importance.

For Archisargidae + Eremochaetidae, and Archocyrtidae + Acroceridae, see notes under Archisargidae (p. 164) and Archocyrtidae (p. 172) respectively.

The determination of the phylogenetic position is difficult on the basis of wing only, but it is hoped that the tree here proposed serves in a degree for future study.

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POSTSCRIPT

Some overlooked papers should have been considered here, of which one is Nartshuk (1995) on Acroceridae [*Juracyrtus kovalevi* Nartshuk and *Archocyrtus gibbosus* Ussatchev] (*Zoosystematica Rossica*, **4**: 313–315). Ansoerge, J., 1996, Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland), *Neue Palaeontologische Abhandlungen*, Dresden, **2**: 1–132, 17 pls, includes only Rhagionidae and unplaced Asilomorpha. It is hoped that these articles will be reviewed collectively some day.

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