

THE MESOZOIC MYCETOPHILOID DIPTERA OF THE FAMILY PLECIOFUNGIVORIDAE

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ABSTRACT: A revision of the family Pleciofungivoridae, known from Jurassic and Lower Cretaceous sediments, has been carried out. The origin and evolution of the pleciofungivorids are discussed, and the problem of their possible descendants among the present-day mycetophiloid Diptera is considered.

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The pleciofungivorids were the largest family of the bibionomorph Diptera throughout the greater part of the Jurassic period. In most of the known Jurassic continental oryctoconoses, this family dominated in abundance and systematic variety among the Diptera, which had evolved outside water, often surpassing, in these parameters, all the remaining nonaqueous Diptera taken together [2, 3].

The oldest representatives of the pleciofungivorids have been described from the basal strata of the Jurassic system in the Issyk-Kul' region (Soguty) [6, 7], where this family, in terms of variety and overall numbers, still did not occupy the dominant position among the bibionomorphs [3]. In materials from Transbaykalia, dated as end of Early—beginning of Middle Jurassic (Kovospasskoye), the pleciofungivorids already were dominant among the bibionomorphs, and they retained this position throughout the remainder of the period in Central Asia, southern Kazakhstan, Central Siberia, Transbaykalia and Mongolia. The greater part of the material needs taxonomic revision. Up till the present, only an insignificant part of the material from Soguty [6, 7] and from the Upper Jurassic sequence of the Karatau Range in the Chirchik area [4, 5, 7] has been described, plus the greater part of the material from the Siberian Jurassic sequence [2]. Pleciofungivorids may also be traced in the Lower Cretaceous interval, but the family became very rare here. Isolated remains are known only from the Neocomian sequence of Baysy (Transbaykalia) [1].

The taxonomic treatment of the materials based on this group from Siberia, carried out recently by the author [2], has required a revision of the earlier-described taxa. He has examined the holotypes of almost all of the species of the pleciofungivorids and representatives of the family "Fungivoritidae" and "Protopleciidae" (see below). Original figures have been made of the wings of the holotypes of the generic type species. Only three species, described from China, remain unknown to the author. Two of them belong to the special genus *Fera* Hong, and one has been described within the genus *Zonesperitus* Rohdendorf.

During the work, it became necessary to review the boundaries of the family and to revise its systematics. The present study is devoted to this end. The revision is essential because part of the generic and species diagnoses have been based on artefacts. The reliability of the illustrations of the venation of several pleciofungivorids, crowded with super-complicated, chaotically arranged, transverse veinlets, has repeatedly raised doubts [8, 9, 11, etc.]. In fact, all the pleciofungivorids have a unique scheme of venation (Figs. 1-4). We have not found any additional veinlets on the type specimens, and RS especially is, in all cases, bifurcate. During the review of about a thousand specimens of still unexamined pleciofungivorids from Soguty, the Karatau, and the Siberian Jurassic sequence, in only three cases did we find weak, super-complicated transverse veinlets: in one case, between R and RS; in another, between RS and the stem M; and in a third, between

M₁₊₂ and M₃. In each case, the super-complicated veinlet was noted only on one wing, and it was most probably either a deformity that is common also in modern Diptera or an artefact.

The problem of the family limits is complicated. In its venation, the wing of the pleciofungivorid is most similar to that of the family Protopleciidae; the pattern of the veinlets in both families is identical. Rohdendorf [7], in placing the pleciofungivorids opposite the protopleciids in his identification table, has indicated that in the first family R₁¹ is short, and at most four times longer than ta, whereas RS₂ is almost always very large and is significantly larger than R₁. According to Rohdendorf, in the protopleciids, R₁ is long and usually more than four times longer than ta, rarely shorter, whereas RS₂ is always shorter than R₁. The features that discriminate both families are insufficiently distinct. The forms assigned by Rohdendorf to the pleciofungivorids, which he has illustrated in Figs. 1012, 1015-1018, 1023 and 1024 (representatives of more than a third of the genera in the family, and mainly type species!), must, according to the diagnoses presented, be included in the Protopleciidae or occupy an intermediate position between both families. The necessity for their clearer demarcation is evident.

The advanced forms of both families, typical of the greater part of the Jurassic period, are easily distinguished, and the key proposed by Rohdendorf for their distribution by families is adequate; but in addition to them, there were also generalized forms, starting points for both families or similar to them, represented at the beginning of Jurassic time. Some of them are preserved in Middle and Upper Jurassic sequences, but are rare here as compared with the advanced forms.

The ancestral group is marked by its small dimensions (length of wing 1.7-3.3 mm); R₁ is long, 3-5 times longer than ta and approximately equal to RS₂; R₁ is long, equal to or longer than RS₂, and sigmoid in shape; the base of M, between the basal cells (M₁) is distinct, although it is often weak (cf. Figs. 2e, f; 3a-c); the antennae are almost unpointed toward the top (their construction is known only in primitive forms from sediments of the end of Early to Late Jurassic age; wings only have been preserved in Lower Jurassic material from Soguty).

From these stem forms spring two phyletic lineages, which separated no later than the Early-Middle Jurassic boundary (Novospasskoye). In one of them, there was an increase in dimensions (wing length up to 7-8 mm), and the venation has changed little; in particular, R₁ and R₂ remain long, M₁ is retained, and the veinlets of the medial system, as in the ancestral group, are strong and a little finer than the radials. The advanced forms are marked by a short RS₂, which is always shorter than R₁, and a very long furca M₁ and M₂, which is more than twice (sometimes 4 times and more) longer than M₃. The antennae (known in a few forms) taper intensely toward the top. This lineage corresponds to the family Protopleciidae. The evolutionary trends, typical of the protopleciids, have been most completely realized in *Mesoplectia* Rohdendorf [7, Fig. 78].

The second phyletic lineage corresponds to the family Pleciofungivoridae. The dimensions remain small (the wing is usually up to 4 mm), the antennae retain the original construction, but the venation changes significantly. R₁ is shortened as a result of a shift in ta toward the base of RS; in the advanced forms, it is often equal to ta and much shorter than RS₂. R₁ becomes shorter and straighter; in the advanced taxa, it is much shorter than RS₂ and almost perpendicular to RS, and often intensely thinned. M₁ is reduced to a weak fold, and the veinlets of the medial system become markedly weakened as compared with those of the radials. The base of the furca M₁ and M₂ is displaced distally, and the furca is often less than two times longer than M₃. The genera *Pleciofungivora* Rohdendorf, *Pleciofungivorella* Rohdendorf, *Fungivorites* Rohdendorf (Fig. 4), and *Chilaroviana* Kovalev possess the most complete assemblage of features of this lineage.

The fact that divergence of the pleciofungivorid and protopleciid lineages had still not taken place at the beginning of Jurassic time and transitions from the ancestral state toward the more advanced forms of both lineages had been smooth in nature does not detract from the necessity for a formal demarcation of the families. There is no sense in merging them together, because the differences between the advanced forms of both lineages are great and correspond to the scale of familial differences accepted in the Diptera. We shall combine the original group with the protopleciids, because they, at least in the wing venation, have retained a great similarity to this group. The new definition of the family Pleciofungivoridae will

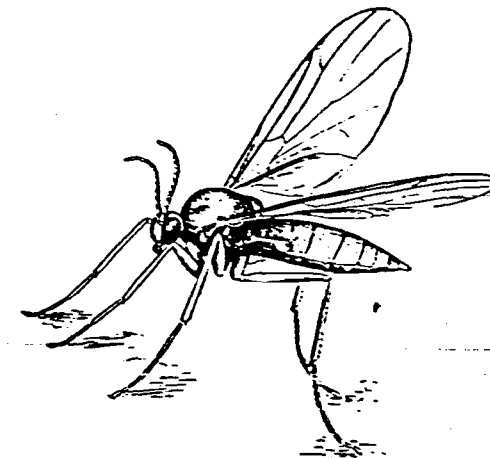


Fig. 1. Reconstruction of *Pleciofungivora* sp.

enable us to distinguish it from the Protopleciidae on the basis of a single feature, the length of R₁. In this instance, the diagnosis has been altered somewhat in comparison with the original [5-7], and some of the forms, earlier included in the family, have been moved into the Protopleciidae.

Splitting of the family into genera is quite complicated, because the morphology of the pleciofungivorids is on the whole monotonous. Here, as in Rohdendorf [4-6], it is based exclusively on the features of the venation, although their assemblage has been somewhat reconsidered. Such a system, however, also reflects the earlier-mentioned evolutionary trends in the venation and remains to a certain extent in dispute. The system, more adequately reflecting the natural state, must take account of features of the construction of the body and other appendages, but the data available on these features are fragmentary. They enable us to give a detailed description of the family as a whole, but still do not make it possible to differentiate the generic and species characteristics.

The following description of the family does not take account of the unusual features of *Fera* Hong, because we are not confident about assigning it to the pleciofungivorids (see below).

FAMILY PLECIOFUNGIVORIDAE Rohdendorf, 1946

Pleciofungivoridae: Rohdendorf, 1946, p. 51.

Allactoneuridae: Rohdendorf, 1938, p. 42 (pars).

Fungivoritidae: Rohdendorf, 1946, p. 79.

Description. Comparatively small Diptera (wing length 1.5-4.0 mm) with slender body, in habit resembling the modern Sciaridae (Fig. 1). Head small, close to the thorax, circular or weakly transverse. Eyes large, circular or transversely oval, minutely faceted, separated frontally above and below the antennae in both fields; frons equal in width to the face or narrower. Ocelli are present, and the ocellar tubercle projects weakly. Cheeks and occiput clearly seen in profile. Antennae attached in the middle of the head or above, in the females usually equal in length to the head and thorax taken together, and in the males, often longer, but not exceeding the length of the body, with 16-17 segments, in small hairs. First and second segments equal in length and width, rounded, usually wider than the segments of the flagellum and more intensely sclerotized. The flagellum is not thinned or tapers weakly toward the top; its segments are oval or cylindrical, gradually becoming shorter from the base to the top of the antenna; distal segments often equal in length and width, but they are not transverse; last segment different in shape: it is either indistinguishable in shape and size from the preceding segment, or is

¹The following abbreviations are used: the basal, middle and terminal sectors of RS (the last corresponds to R₃) are denoted as R₁, RS₂ and RS₃ and the corresponding sectors of M₁₊₂, as M₁, M₂ and M₃ (Fig. 2f).

smaller or longer, and spindle-shaped, often with a transverse suture or slope in the upper half; in the latter case, it must be regarded as the product of incomplete merger of the 16th and 17th segments. Palps (Fig. 2b) usually distinctly shorter than the height of the head, rarely a little longer, in four segments; the first and second segments are shorter than the rest. Proboscis much shorter than the head, soft, with a wide oral disc.

Thorax moderately convex in profile from above, with the anterior slope steeper than the posterior, covered with indistinct hairs, without strong bristles. Scutellum short, ridge-like, and weakly projecting.

Wings (Figs. 1-4) quite broad, oval, usually with weakly developed anal lobe, rounded axillary angle greater than 90° , and occipital wing scale in the form of a projection of the anterior margin of the basalia. Membrane often with a vague stigmal patch on the costal margin at the top of R_1 and R_2 , in other places without any such mark, evenly covered with microtrichia, not massed into rows. Costal (C) and radial veinlets (except for R_2) densely covered with small hairs. Venation moderately costalized. All the veinlets, except CuP and An_1 , complete. C disappears between the tops of R_2 and M_1 . There is a vena humeralis. Sc runs into C, comprises about one-third of the wing length, and usually tapers toward the top. Sc_2 is not expressed. Remigium with a break or sharp bend at the base. R_1 is thicker than all the remaining veinlets, and equal to 0.7-0.8 times the wing length. RS branches off at about the level of the end of the basal third of the wing, with a band or break at the point of junction with ta , and, farther on, to the top of the wing, usually arcuately curved, repeating the bend in the costal margin, and ending in front of the top of the wing. A single anterior branch (R_2) extends at an angle from RS, passing into C immediately behind R_1 ; it is usually thinner than RS_3 (R_3). RS_1 at a maximum is five times longer than ta and shorter than RS_2 , and exceptionally equal to it. Veinlet ta is always present and is almost vertical. The veinlets of the medial system are much weaker than the radials. M is three-branched and includes veinlets M_1 and M_2 , forming a furca, and M_3 . The proximal portion of M (M_1) has been reduced as compared with the distal section, and in the advanced forms has the form of a scarcely perceptible fold, so that the main cells are in fact merged. The furca of M_1 and M_2 is somewhat more proximal than furca RS, and less than a quarter longer than M_3 ; M_1 ends just behind the top of the wing. M_3 passes out from the stem of M much more proximally than ta , is connected with Cu only by the transverse mcu , and is almost straight; its basal sector tb (up to mcu) is set at an angle to the long terminal sector, is very short or completely disappears, and then M_3 starts from the point where M and mcu join. The transverse veinlet mcu is rotated. CuA is weaker than the radial veinlets, but stronger than the radials, bending arcuately in the top half toward the posterior margin of the wing. CuP is clearly adjacent to CuA . Veinlet An_1 is almost straight and disappears, without reaching the margin of the wing. Halteres with a relatively short stem.

Foot long, cursorial, of simple construction, the 2nd-5th segments of the anterior tarsus rarely expanded. Posterior foot a little longer than the median, and the median longer than the anterior. Tibia usually insignificantly, and rarely 1.5 times, longer than the femur. Coxa large, but not elongated, not longer than half the femur; the anterior coxa a little shorter than the median and posterior. Tibia on top with ventral soft spurs (usually poorly visible in fossil material), the length of which is normally not greater than the diameter of the tibia (Fig. 2c); the spur formula is evidently always 1:2:2. The surface of the tibia, besides spurs, bears very small hairs, which are always shorter than the diameter of the tibia; the strongest hairs form a longitudinal-like row on the dorsal surface of the posterior tibia; there are sometimes hairs on the ventral surface of the tarsal segments. Tarsus usually equal to tibia, the first segment usually approximately equal to the overall length of the remainder.

Abdomen longer than head and thorax together, with well-developed tergites and sternites, slightly contracted toward the top from V or one of the last segments, and sometimes also weakly tapered at the base (segments I and II). Between tergites I and II and/or the corresponding sternites, there is often a sclerotized band, bordered in front and behind by a membrane, which is the posterior portion of tergite I (sternite) or the anterior portion of tergite II (sternite). Segment I is shorter than the subsequent ones. In the male, there are eight visible segments, the last being little distinguishable from the preceding ones. The genital complex is not wider than the abdomen, is oval or transverse, and includes massive conical gonocoxites and shorter cylindrical gonostyles passing out from their crests and ending in

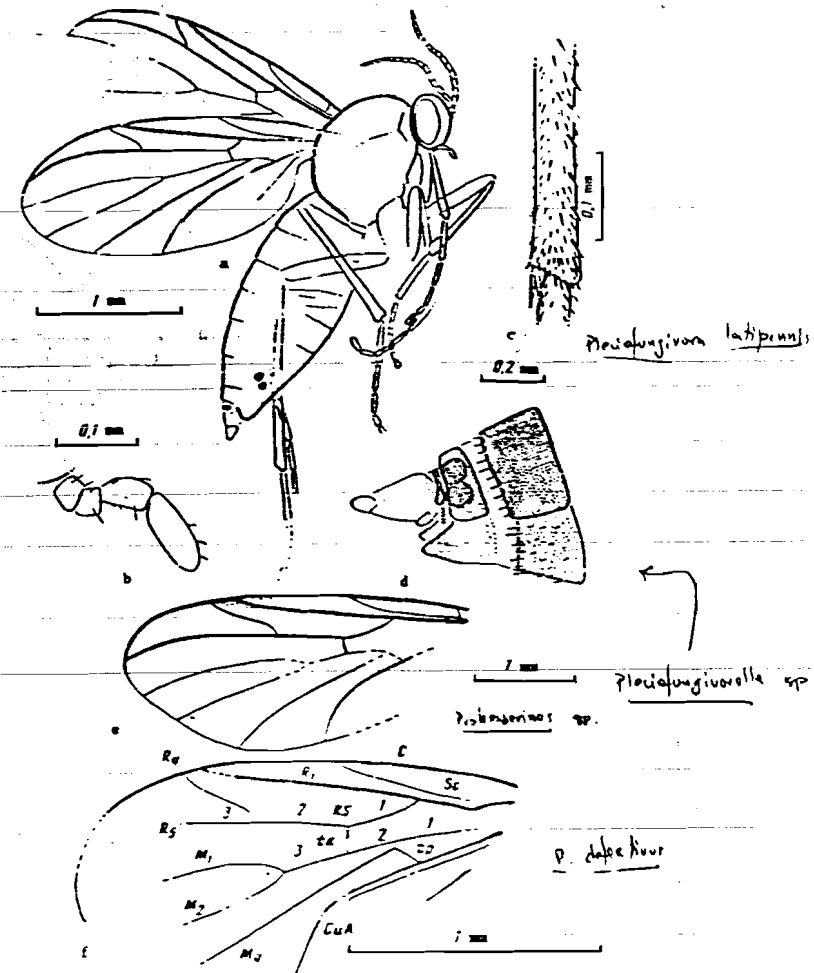


Fig. 2. Representatives of the family Pleciofungivoridae: a, b) *Plecofungivora latipennis* Rohdendorf; Spec. PIN No. 2903/1447, female: a) general appearance, b) palps; c) *Plecofungivorella proxima* Rohdendorf; Spec. No. 2957/1312, top of posterior tibia; d) *Plecofungivorella* sp., Spec. no. 2784/138, female, top of abdomen; e) *Pronesperiurus acuminatus* Rohdendorf; holotype, No. 2452/680, wing; Chizkent area, Karata; Range; Upper Jurassic, Karabastau Group; f) *P. defessus* (Rohdendorf); holotype, No. 371/913, wing; Issyk-Kul' area, Sogvuty Gorge; Lower Jurassic, Dzhal'sk group. Normal symbols for veinlets.

minute denticles. The female has no telescopic ovipositor; the membranes between the distal segments are not longer than those between the proximal segments. Segment VIII has been sclerotized more intensely than the preceding segments and is conical; the tergite is shorter than the preceding ones and the true sternite; the latter, on the other hand, is sometimes longer than the preceding ones, with a deep notch on the posterior margin. Tergite IX is very short. The cerci are soft and laminar, normally

²The venation nomenclature is that according to Hennig [9]. However, it is possible that the anterior branch of RS corresponds to R_{2+3} , whereas R_2 has disappeared or has merged with R_3 . Following Hennig, we shall regard the posterior branch of M as M_3 , believing that M_2 has disappeared.

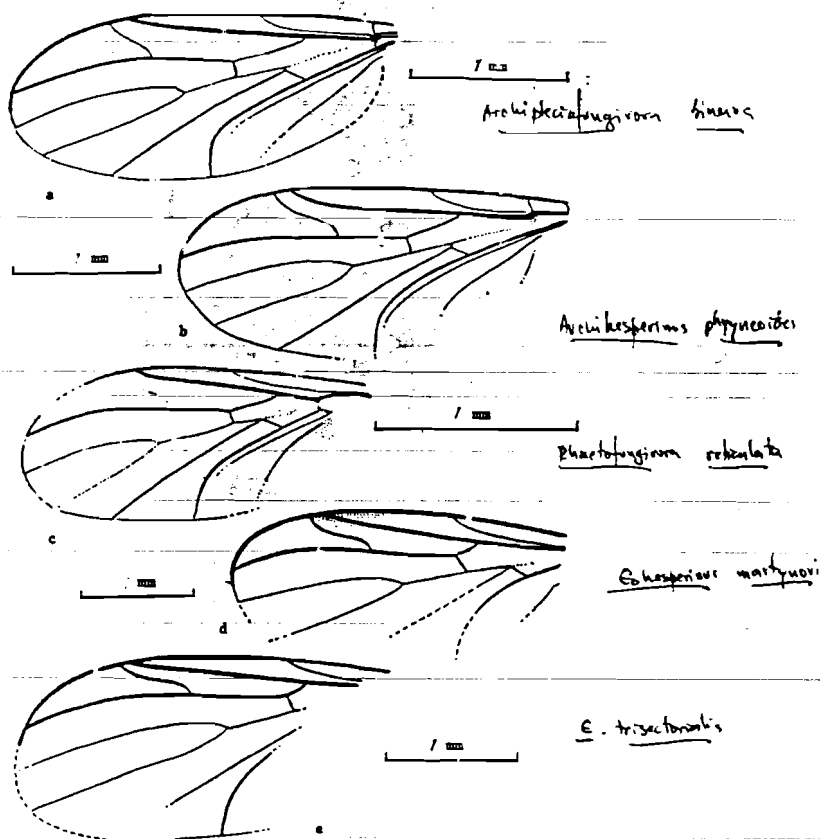


Fig. 3. Representative of family Pleciofungivoridae, wings: a) *Archiplectrofungivora binerva* Rohdendorf; Holotype No. 358/41; b) *Archihesperinus phryneoides* Rohdendorf; Holotype No. 371-912; c) *Rhaetofungivora reticulata* Rohdendorf; Holotype No. 358/123; Issyk-Kul' area; Soguty Gorge; Lower Jurassic, Dzhal'sk Group; d) *Eoheperinus martynovi* Rohdendorf; Holotype No. 2452/289; e) *Eoheperinus trisectorialis* (Rohdendorf); Holotype No. 2452/673; Chikment area, Karatau Range; Upper Jurassic, Karabastau group.

not longer than segment VIII, and twofold; the terminal segment is oval and is shorter than the basal one. There are two rounded, sclerotized spermathecae (Fig. 2a).

Composition. *Archihesperinus* Rohdendorf and *Rhaetofungivora* Rohdendorf, Lower Jurassic of Issyk-Kul' area; *Archiplectrofungivora* Rohdendorf, Lower-Middle Jurassic of Central Asia and Siberia; *Bryanka* Kovalev, Lower-Middle Jurassic of Siberia; *Matilia* Kovalev and *Rohdendorffomyia* Kovalev, Lower-Middle Jurassic of Transbaykalia; *Willihennigia* Kovalev, Lower-Upper Jurassic of Siberia; *Plectrofungivora* Rohdendorf, *Plectrofungivorella* Rohdendorf, and *Proheperinus* Rohdendorf, Lower-Upper Jurassic of Siberia, Central Asia, and Kazakhstan; *Fera* Hong, Middle Jurassic of northern China; *Eoheperinus* Rohdendorf, Middle-Upper Jurassic of Siberia and Kazakhstan; *Krasnoyarskia* Kovalev, Middle-Upper Jurassic of Transbaykalia; and *Fungivorella* Kovalev, Upper Jurassic of Chikment area. A huge amount of undescribed material comes from the Jurassic sequence of Central Asia and Mongolia and from the Neocomian strata of Transbaykalia.

Comparison. This family is distinguished from the Protopleciidae by the short

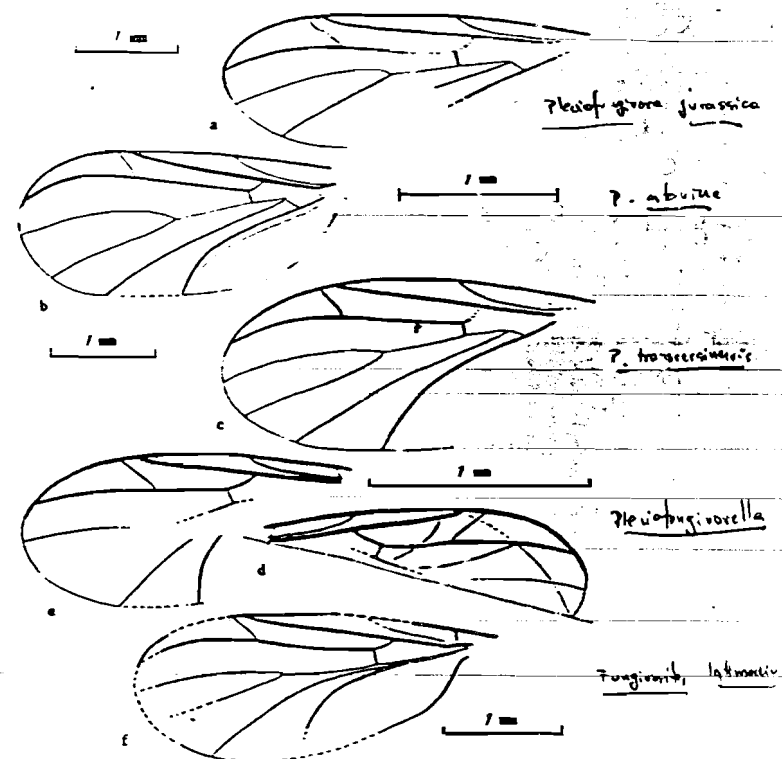


Fig. 4. Representatives of the Pleciofungivoridae, wings: a) *Plectrofungivora jurassica* (Rohdendorf); Holotype No. 2452/356; b) *P. aburue* (Rohdendorf); Holotype No. 340/167; c) *P. transversinervis* (Rohdendorf); Holotype No. 2452/358; d, e) *Plectrofungivorella binerva* Rohdendorf; d) Holotype No. 22/1-7; e) reconstruction of venation; f) *Fungivorella latimaculata* Rohdendorf; Holotype No. 2452/548 (wing split along median veinlets and CuA, as a result of which the bases of these veinlets are closer together than was the case in the living insect, and mCu is not seen); Chikment area, Karatau Range; Upper Jurassic, Karabastau group.

RS1; it is distinguished from the modern family Bolitophilidae, with its similar venation patterns, by the longer M3.

Remarks. In a further review, only those earlier-described genera are considered whose diagnoses require refinement or revision. A determinative table for the genera of the family and descriptions of seven genera from the Jurassic sequence of Siberia has been given in a publication by the author [2].

The genera *Rhaetofungivorella* Rohdendorf, *Archiplectrofungivora* Rohdendorf, *Palaeoheperinus* Rohdendorf and *Protopleciidoneura* Rohdendorf have been described from Soguty [6]; as a result of a revision of the type material and refinement of the diagnosis of the family, they have been transferred to the family Protopleciidae.

The venation of the pleciofungivorids, described from the Middle Jurassic sequence of northern China (both species of *Fera* Hong and *Eoheperinus gracilis* Hong), is unusual: Sc is unusually long for the mycetophyllids; RS branches in front of the very top of the wing, and, in this case, R₁ terminates farther from R₂ than in all the other pleciofungivorids [10, Figs. 102-104]. The systematic position of these forms is uncertain. It is possible that they should be placed in a separate

family. It is also possible, however, that the venation has not been completely accurately illustrated.

Rohdendorf [7], on the basis of Tillyard's information [13] on an undescribed dipterous insect from the lower Liassic sequence of England (Brit. Mus. (Nat. Hist.) Spec. No. 1.10458), has assigned it to the pleciofungivorids. However, from its venation, it may be assigned both to this family and to the Protopleciidae and the Cro-saphididae. Tillyard's statement that the posterior tibia is 2.2 times longer than the femur almost destroys the grounds for including this form in the Pleciofungivoridae.

Genus *Prohesperinus* Rohdendorf, 1946

Prohesperinus: Rohdendorf, 1946, p. 56.

Rhaetofungivorodes: Rohdendorf, 1962, p. 230.

Type species. *P. abdominalis* Rohdendorf, 1946; Upper Jurassic; Chimkent area.

Diagnosis (Fig. 2e, f). Sc terminates at the level of the anterior end of ta or more distally. R₁ is more than three times longer than ta; RS₂ is insignificantly longer than R₁. Veinlet R₁ is long, less than three times shorter than RS₃, lies at an angle of not more than 45° to RS, and is sigmoid in shape. The M₁₊₂ furca is at least three times longer than M₃.

Species composition. *P. defectivus* (Rohdendorf, 1962) comb. nov., from the Lower Jurassic sequence of the Issyk-Kul' area, the type species, and possibly *P. pediculi* Rohdendorf, 1964, from the Upper Jurassic of the Chikment area (in the single specimen from which the species has been described, the wing is badly preserved and the M₁ and M₂ furca is not visible).

Comparison. It is distinguished from the most similar *Rhaetofungivora* by the long M₁ and M₂ furca and from *Archihesperinus* and *Archiplectiofungivora*, by its long Sc.

Remarks. The wing venation of *Rhaetofungivorodes defectivus*, the only representative of that genus, has been inaccurately illustrated in the original description [6]: R₁ passes out more distally than is shown in the figure. In fact, the venation of *P. defectivus* (Fig. 2f), like that of *P. abdominalis*, is distinguished by its specific features alone. On this basis, the name *Rhaetofungivorodes* is placed in the synonymy of *Prohesperinus*. The construction of the body is known only for the Late Jurassic species of *Prohesperinus*.

Genus *Archihesperinus* Rohdendorf, 1962

Type species. *A. phryneoides* Rohdendorf, 1962; Lower Jurassic, Issyk-Kul' area.

Diagnosis (Fig. 3b). Sc ends close to the middle of R₅1. Veinlet R₁, which begins at the base of R₄, forms quite a marked bend toward the anterior margin of the wing. R₅1 is at least twice as long as ta; RS₂ is slightly longer than R₅1. Veinlet R₁ is strong and long, a little less than half the length of RS₃, forms an angle of less than 45° with RS, and is sigmoid in shape. M₃ is longer than M₂, and the M₁₊₂ furca is long and approximately twice the length of M₃.

Species composition. Type species.

Comparison. Given in the diagnosis of *Archiplectiofungivora*.

Remarks. It is possible that this genus should be united with *Archiplectiofungivora*. The construction of the body in both genera is unknown.

Genus *Archiplectiofungivora* Rohdendorf, 1962

Type species. *A. binerva* Rohdendorf, 1962; Lower Jurassic, Issyk-Kul' area.

Diagnosis (Fig. 3a). Sc terminates close to the middle of R₅1. Veinlet R₁ is almost straight. R₁ is less than half the length of RS₃ and forms an angle of about 45° with RS. Remainder as for *Archihesperinus*.

Species composition. Besides the type species, an undescribed form from the Middle Jurassic of the Chulym-Yenisey Basin [2].

Comparison. Distinguished from the very similar *Archihesperinus* by its short R₁ (in *Archihesperinus*, R₁ is less than half the length of RS₃) and the straight R₁.

Genus *Rhaetofungivora* Rohdendorf, 1962

Type species. *R. reticulata* Rohdendorf, 1962; Lower Jurassic: Issyk-Kul' area.

Diagnosis (Fig. 3c). Sc terminates at the anterior end of ta or more distally. R₅1 is more than twice as long as ta, and section RS₂ is insignificantly longer than R₅1. Veinlet R₁ is long, more than half the length of RS₃, with which it forms an angle not greater than 45°, and it is sigmoid in shape. The M₁₊₂ furca is approximately twice (distinctly less than three times) the length of M₃.

Species composition. Type species.

Comparison. It differs from the most similar genus *Prohesperinus* in its shorter M₁₊₂ furca, and from *Archiplectiofungivora* and *Archihesperinus* in the length of Sc.

Remarks. Fifteen species of this genus have been described from the basal Lower Jurassic of the Issyk-Kul' area [6, 7]. As a preliminary study of the type specimens has shown, all these species belong to the Protopleciidae.

Genus *Eohesperinus* Rohdendorf, 1946

Eohesperinus: Rohdendorf, 1946, p. 60.

Eopachyneura: Rohdendorf, 1946, p. 57.

Type species. *E. arctynovi* Rohdendorf, 1946; Upper Jurassic; Chikment area.

Diagnosis (Fig. 3d, e). Sc terminates at the anterior end of ta or more distally. R₅1 is short, more than twice as long as ta and at least three times shorter than RS₂. Veinlet R₁ long, approximately half the length of RS₃, with which it forms an angle of 45°, and sigmoid. The M₁₊₂ furca is not less than 2.5 times longer than M₃.

Species composition. The type species, *E. trisectoralis* (Rohdendorf, 1946) comb. nov. and *E. ussuri* Rohdendorf, 1964, from the Upper Jurassic of the Chikment area; and *E. sibiricus* Kovalev, 1985, from the Middle Jurassic of the Chulym-Yenisey basin.

Comparison. Differs from *Plectiofungivora*, *Plectiofungiarella* and *Fungivorites*, which also have a short R₅1, in the long R₁.

Remarks. As the main feature, characterizing the monotypic genus *Eopachyneura*, Rohdendorf points to the presence of an additional branch in RS [5, Fig. 63]. This branch is an artefact. After its removal, the basis for recognizing *Eopachyneura* disappear, and this name is regarded as a synonym of *Eohesperinus*. The wing venation of the holotype of *E. trisectoralis* is illustrated in Fig. 3e. *E. gracilis* Hong, 1983, as may be judged from the description and illustration [10], cannot be assigned to *Eohesperinus* (see remarks in the diagnosis of the family).

Genus *Plectiofungivora* Rohdendorf, 1938

Plectiofungivora: Rohdendorf, 1938, p. 42.

Allactoneurites: Rohdendorf, 1938, p. 43.

Polynuriscus: Rohdendorf, 1946, p. 52.

Transversiplectis: Rohdendorf, p. 53.

Type species. *P. latipennis* Rohdendorf, 1938; Upper Jurassic; Chikment area.

Diagnosis (Figs. 1; 2a, b; 4a-c). Sc terminates at the level of the anterior end of ta or more distally. R₁ is almost straight. R₅1 is short, not more (and usually distinctly less) than 2.5 times longer than ta and at most half the length of RS₂. Veinlet R₁ appears almost immediately in front of the level of the end of R₄, which is at most, half the length of RS₃, with which it usually makes an angle of not less than 45°, and is often almost straight. M₃ is longer than M₂, and the M₁₊₂ furca is comparatively short, being 1.5-2.5 times longer than M₃.

Species composition. The type species, *P. jurassica* (Rohdendorf, 1938) comb. nov., *P. atavina* (Rohdendorf, 1946) comb. nov., *P. major* Rohdendorf, 1946, and *P. transversinervis* (Rohdendorf, 1946) comb. nov. from the Upper Jurassic of the Chirkent area; *P. burjatika* Kovalev, 1985, and *P. transbaikalia* Kovalev, 1985, from the Lower-Middle Jurassic sequence of Transbaikalia; and *P. yenisseyica* Kovalev, 1985, from the Middle Jurassic of the Chulym-Yenisey basin [2].

Comparison. Close to *Plectrofungivorella* and *Fungivorites*. Distinguished from the former by the long Sc, and from the latter by the longer M_{1+2} furca.

Remarks. The monotypic genera *Transversiplecia* and *Polyneurisca* were separated on the basis of an erroneous interpretation of the venation. The transverse veinlet within Sc in *T. transversinervis* [5, Fig. 57] is an artefact (a strand of detritus, intersecting the wing). The oblique transverse veinlets between C and RS in *Polyneurisca atavina* [5, Fig. 56] have turned out to be irregularities in the rock surface, and in places, dark punctate inclusions of organic matter; they have been seen only in one of two wings. The true venation of the wings of *P. atavina* (Fig. 4b) and *T. transversinervis* (Fig. 4c) is of the same type as in *Plectrofungivora*, so that the names *Polyneurisca* and *Transversiplecia* are regarded here as synonyms of *Plectrofungivora*.

In the description of *Allaotoneurites*, with its single species, *A. jurassica*, Rohdendorf indicated that this genus is distinguished from *Plectrofungivora* by the "... differing proportions of the veinlets -- a longer RS, and a different, narrower wing" [4, p. 44]. In 1938, when both genera were described, each of them was known from a single representative. The scope of *Plectrofungivora* has now been expanded. Its representatives, described after 1938, within the genera *Plectrofungivora*, *Polyneurisca* and *Transversiplecia* and also species from Siberia [2], in respect to the features listed by Rohdendorf, have an intermediate position between *A. jurassica* and *P. litipennia* and these features do not have generic rank. Therefore, the name *Allaotoneurites* is also regarded as a synonym of *Plectrofungivora*. The wing venation of *P. jurassica* is illustrated in Fig. 4a.

Genus *Fungivorites* Rohdendorf, 1938

Type species. *F. latimediis* Rohdendorf, 1938; Upper Jurassic; Chirkent area.

Diagnosis (Fig. 4f). The M_{1+2} furca is less than 1.5 times longer than M_3 . The remaining features are as in *Plectrofungivora*.

Species composition. Type species.

Comparison. This genus differs from *Plectrofungivorella* in its long Sc.

Remarks. The original diagnosis of the genus and the accompanying figure [4, Fig. 18] contain errors: R_1 is illustrated as being longer than it in fact is; R_2 is not shown; the statement that the femur is markedly inflated does not agree with reality (it is thin, as in the remaining plectrofungivorids). The family Fungivoritidae in its original sense is heterogeneous. It includes representatives of the families Plectrofungivoritidae (*Fungivorites*), Plectromimidae, and Mesosciophilidae [2]. The species *F. indistinctus* Rohdendorf, 1946, may not be assigned either to *Fungivorites* or to the family Plectrofungivoritidae, because R_1 in it almost reaches the top of the wing. Statz [12], who did not realize that the name *Fungivorites* had already been used as a generic taxon, described under the name *Fungivorites problematicus*, an unusual representative of the Diptera from the Miocene sequence of Western Europe. This insect clearly bears no relationships to the mycetophiloids, but most probably belongs to the superfamily Psychodoidea. The name *Fungivorites* should not be used in future for this insect.

Genus *Plectrofungivorella* Rohdendorf, 1946

Type species. *P. binerva* Rohdendorf, 1946; Upper Jurassic; Chirkent area.

Diagnosis (Figs. 4d, e). Sc terminates freely not farther than the middle of RS_1 , and rarely a little more distally, but always clearly does not reach the level of the anterior end of ra . The RS_3 sector is very weakly curved. The M_{1+2} furca is more than 1.5 times longer than M_3 . The remaining features are as for *Plectrofungivora* and *Fungivorites*.

Species composition. The type species, *P. brevisubcosta* Rohdendorf, 1946, and *P. proxima* Rohdendorf, 1946, from the Upper Jurassic of the Chirkent area; *P. itchevica* Kovalev, 1985, and *P. tugnica* Kovalev, 1985, from the Lower-Middle Jurassic sequence of Transbaikalia; *P. kraenovarica* Kovalev, 1985, from the Middle Jurassic of the Chulym-Yenisey basin; and *P. udaensis* Kovalev, 1985, from the Middle-Upper Jurassic sequence of Transbaikalia.

Comparison. Genus differs from the similar *Plectrofungivora* and *Fungivorites* in the short Sc.

Remarks. The principal generic feature of *Plectrofungivorella* Rohdendorf [5, 6] has been considered to be the presence of two anteriorly extending branches of RS (three-branched RS). This feature is an artefact. In the holotypes of *P. binerva* (Fig. 4d) and *P. proxima*, the wing is so constructed that its posterior margin lies beneath the anterior. The veinlet, accepted in the original descriptions as the anterior ancillary branch of RS, in fact corresponds to CuA and the venation is actually included in the generic scheme. Here, the generic status of *Plectrofungivorella* is retained, because the short Sc, which distinguishes the species of this genus from its close relatives, seems to be a stable feature of generic rank.

THE EVOLUTION AND GENERIC RELATIONSHIPS OF THE PLECTROFUNGIVORIDS

As already stated, the family was a derivative of the protopleciids. Its morphological evolution, because of lack of information about the body construction, may only be traced through the wing venation. The early Liassic plectrofungivorids possessed the most primitive venation. During its subsequent evolution, the following trends may be clearly recognized: shortening of Sc, RS_1 , and the M_{1+2} furca, shortening and straightening of R_2 , and an increase in the angle between this furca and RS . From an analysis of these trends and firm data on the geological age, the appended scheme of phylogenetic relationships of the genera is given (Fig. 5). It shows, first, that the forms with a complete assemblage of the listed apomorphs (*Plectrofungivora* and *Plectrofungivorella*) appeared at the end of the Early and the beginning of the Middle Jurassic, and, second, that even at the end of Jurassic time, primitive forms (*Prohesperinus*) also continued to exist along with such forms. Progressive trends in the wing venation were not always achieved simultaneously. Some genera combined archaic and progressive features; for example, the long R_2 with a very short RS_1 was retained in *Eohesperinus*.

An undoubted derivative of the plectrofungivorids was the family Plectromimidae, first recorded in the upper Liassic sequence [7]. The primitive plectromimids are distinguished from the plectrofungivorids by a unique apomorphy (the absence of R_2). Evidently, the reduction of R_2 , associated with miniaturization (the plectromimids are usually smaller than the plectrofungivorids), could have taken place in different groups of plectrofungivorids independently, and the plectromimids do not represent a monophyletic group [2].

There are no reliable data on other direct descendants of the plectrofungivorids. Rohdendorf [7] has stressed that this family is the ancestor of many Cenozoic groups of fungivoroids (= Mycetophiloidea) and probably also of the entire superfamily Bibionoidea. The validity of this view has subsequently been repeatedly disputed [9, 11].

There are, in fact, no grounds for believing that the plectrofungivorids are the original forms of the bibionoids. The recent bibionoids of the families Hesperinidae and Plectridae, closest to the prototype, are distinguished by plesiomorphies of the venation (a distinct M_1 , a long M_2 and M_3 furca (both families), a complete An (Hesperinidae), and very long Sc and R_2 (Plectridae)). Direct derivatives of the plectrofungivorids have been considered by Rohdendorf [5] to be the modern families of mycetophiloids, Keroplatidae, Macroceridae and Dicoxyiidae, although in that same work, it was pointed out that in certain features of the venation, the plectrofungivorids are more apomorphic than the dicoxyiids, without making any firm comments about such features. The plesiomorphies of the venation of these recent families, which distinguish them from the plesiofungivorids have been discussed in detail by Hennig [9], who has demonstrated the impossibility of deriving them directly from the plectrofungivorids. Hennig's conclusions are illustrated with complete confidence.

Among the modern mycetophiloids, the venation pattern of the plectrofungivorids most closely corresponds to that in the family Bolitophilidae and the genus *Pterogymna* Freeman of uncertain systematic position. Quite a close relationship between the bolitophilids and the plectrofungivorids is not excluded, as is indicated by the construction of the appendages of the bolitophilids (shorter than in other modern mycetophiloids), the coxa, and the weakly developed spurs on the tibia. However, the differences in the venation of the bolitophilids from that of the plectrofungivorid pattern bear the character of plesiomorphs: An₁ reaches the margin of the wing, the M_{1+2} furca is very long. Matile [11] mentions yet another difference, the presence in the bolitophilids of a short Sc; veinlet between Sc and R_2 , which belongs to the original venation pattern of the dipterid wing. In the plectrofungivorids, this veinlet has been lost (in reviewing very well-preserved material from the Middle Jurassic sediments from the Chulym-Yenisey basin, this veinlet has not been found in a single fossil, although it is readily observed in the mycetophiloids of the family Mesosci-

family. It is also possible, however, that the venation has not been completely accurately illustrated.

Rohdendorf [7], on the basis of Tillyard's information [13] on an undescribed dipterous insect from the lower Liassic sequence of England (Brit. Mus. (Nat. Hist.) Spec. No. 1.10458), has assigned it to the pleciofungivorids. However, from its venation, it may be assigned both to this family and to the Protopleciidae and the Crocaphididae. Tillyard's statement that the posterior tibia is 2.2 times longer than the femur almost destroys the grounds for including this form in the Pleciovungivoridae.

Genus *Prohesperinus* Rohdendorf, 1946

Prohesperinus: Rohdendorf, 1946, p. 56.

Rhaetofungivorodes: Rohdendorf, 1962, p. 230.

Type species. *P. abdominalis* Rohdendorf, 1946; Upper Jurassic; Chirkent area.

Diagnosis (Fig. 2e, f). Sc terminates at the level of the anterior end of ta or more distally. R₁ is more than three times longer than ta; RS₂ is insignificantly longer than R₁. Veinlet R₁ is long, less than three times shorter than RS₃, lies at an angle of not more than 45° to RS, and is sigmoid in shape. The M₁ and M₂ furca is at least three times longer than M₃.

Species composition. *P. defectivus* (Rohdendorf, 1962) comb. nov., from the Lower Jurassic sequence of the Issyk-Kul' area, the type species, and possibly *P. pedalis* Rohdendorf, 1964, from the Upper Jurassic of the Chirkent area (in the single specimen from which the species has been described, the wing is badly preserved and the M₁ and M₂ furca is not visible).

Comparison. It is distinguished from the most similar *Rhaetofungivora* by the long M₁ and M₂ furca and from *Archihesperinus* and *Archipleciofungivora*, by its long Sc.

Remarks. The wing venation of *Rhaetofungivorodes defectivus*, the only representative of that genus, has been inaccurately illustrated in the original description [6]: R₁ passes out more distally than is shown in the figure. In fact, the venation of *P. defectivus* (Fig. 2f), like that of *P. abdominalis*, is distinguished by its specific features alone. On this basis, the name *Rhaetofungivorodes* is placed in the synonymy of *Prohesperinus*. The construction of the body is known only for the Late Jurassic species of *Prohesperinus*.

Genus *Archihesperinus* Rohdendorf, 1962

Type species. *A. phrynoidea* Rohdendorf, 1962; Lower Jurassic, Issyk-Kul' area.

Diagnosis (Fig. 3b). Sc ends close to the middle of R₁. Veinlet R₁, which begins at the base of R₂, forms quite a marked bend toward the anterior margin of the wing. R₁ is at least twice as long as ta; RS₂ is slightly longer than R₁. Veinlet R₂ is strong and long, a little less than half the length of RS₃, forms an angle of less than 45° with RS, and is sigmoid in shape. M₃ is longer than M₂, and the M₁₊₂ furca is long and approximately twice the length of M₃.

Species composition. Type species.

Comparison. Given in the diagnosis of *Archipleciofungivora*.

Remarks. It is possible that this genus should be united with *Archipleciofungivora*. The construction of the body in both genera is unknown.

Genus *Archipleciofungivora* Rohdendorf, 1962

Type species. *A. binerva* Rohdendorf, 1962; Lower Jurassic, Issyk-Kul' area.

Diagnosis (Fig. 3a). Sc terminates close to the middle of R₁. Veinlet R₁ is almost straight. R₁ is less than half the length of RS₃ and forms an angle of about 45° with RS. Remainder as for *Archihesperinus*.

Species composition. Besides the type species, an undescribed form from the Middle Jurassic of the Chulym-Yenisey Basin [2].

Comparison. Distinguished from the very similar *Archihesperinus* by its short R₁ (in *Archihesperinus*, R₁ is less than half the length of RS₃) and the straight R₁.

Genus *Rhaetofungivora* Rohdendorf, 1962

Type species. *R. reticulata* Rohdendorf, 1962; Lower Jurassic; Issyk-Kul' area.

Diagnosis (Fig. 3c). Sc terminates at the anterior end of ta or more distally. R₁ is more than twice as long as ta, and section RS₂ is insignificantly longer than R₁. Veinlet R₁ is long, more than half the length of RS₃, with which it forms an angle not greater than 45°, and it is sigmoid in shape. The M₁₊₂ furca is approximately twice (distinctly less than three times) the length of M₃.

Species composition. Type species.

Comparison. It differs from the most similar genus *Prohesperinus* in its shorter M₁₊₂ furca, and from *Archipleciofungivora* and *Archihesperinus* in the length of Sc.

Remarks. Fifteen species of this genus have been described from the basal Lower Jurassic of the Issyk-Kul' area [6, 7]. As a preliminary study of the type specimens has shown, all these species belong to the Protopleciidae.

Genus *Eohesperinus* Rohdendorf, 1946

Eohesperinus: Rohdendorf, 1946, p. 60.

Eopachyneura: Rohdendorf, 1946, p. 57.

Type species. *E. arctynovi* Rohdendorf, 1946; Upper Jurassic; Chirkent area.

Diagnosis (Fig. 3d, e). Sc terminates at the anterior end of ta or more distally. R₁ is short, more than twice as long as ta and at least three times shorter than RS₂. Veinlet R₁ long, approximately half the length of RS₃, with which it forms an angle of 45°, and sigmoid. The M₁₊₂ furca is not less than 2.5 times longer than M₃.

Species composition. The type species, *E. trisectoralis* (Rohdendorf, 1946) comb. nov. and *E. ueseri* Rohdendorf, 1964, from the Upper Jurassic of the Chirkent area; and *E. sibiricus* Kovalev, 1985, from the Middle Jurassic of the Chulym-Yenisey basin.

Comparison. Differs from *Pleciofungivora*, *Pleciofungiarella* and *Fungivorites*, which also have a short R₁, in the long R₁.

Remarks. As the main feature, characterizing the monotypic genus *Eopachyneura*, Rohdendorf points to the presence of an additional branch in RS [5, Fig. 63]. This branch is an artefact. After its removal, the basis for recognizing *Eopachyneura* disappear, and this name is regarded as a synonym of *Eohesperinus*. The wing venation of the holotype of *E. trisectoralis* is illustrated in Fig. 3e. *E. gracilis* Hong, 1983, as may be judged from the description and illustration [10], cannot be assigned to *Eohesperinus* (see remarks in the diagnosis of the family).

Genus *Pleciofungivora* Rohdendorf, 1938

Pleciofungivora: Rohdendorf, 1938, p. 42.

Allaenoneurites: Rohdendorf, 1938, p. 43.

Polyneurites: Rohdendorf, 1946, p. 52.

Transversiplexis: Rohdendorf, p. 53.

Type species. *P. latipennis* Rohdendorf, 1938; Upper Jurassic; Chirkent area.

Diagnosis (Figs. 1; 2a, b; 4a-c). Sc terminates at the level of the anterior end of ta or more distally. R₁ is almost straight. R₁ is short, not more (and usually distinctly less) than 2.5 times longer than ta and at most half the length of RS₂. Veinlet R₁ appears almost immediately in front of the level of the end of R₂, which is at most, half the length of RS₃, with which it usually makes an angle of not less than 45°, and is often almost straight. M₃ is longer than M₂, and the M₁₊₂ furca is comparatively short, being 1.5-2.5 times longer than M₃.

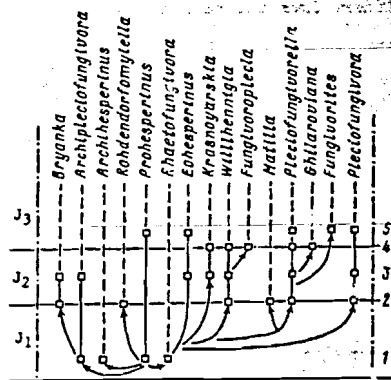


Fig. 5. Sketch of the phylogenetic relationships of the Jurassic Pleciofungivoridae. Symbols: 1) Lower Jurassic of the Issyk-Kul' area (Soguty Gorge); 2) Lower-Middle Jurassic of Transbaykalia (Novospasskoye, Bryanka); 3) Middle Jurassic of Chul'-Yenisey Basin (Kubekovo); 4) Middle-Upper Jurassic of Transbaykalia (Uda River); 5) Upper Jurassic of southern Kazakhstan (Karatau Range).

philidae from this same locality). The venation in *Pterogymnus* [9, Fig. 91] more closely corresponds to the pleciofungivorid pattern (An_1 is incomplete, the M_{1+2} furca is comparatively short, but R_1 does not merge into C, but into R_2 , as in certain bolitophilids, but not in the pleciofungivorids. This unusual genus may have been the product of both the pleciofungivorids and the bolitophilids.

Thus, there are no sufficiently weighty arguments that point to the origin of any of the Cenozoic subdivisions of the mycetophiloids from the pleciofungivorids. However, the carefully framed proposition about the "sister" relationships between the Mesozoic Pleciofungivoridae along with the Mesosclerophilidae and the modern mycetophiloids (including the Sciaridae) possibly is well founded. Matile [11] believes that among the modern mycetophiloids the Ditomyiidae and certain genera of indeterminate position close to *Heterotricha* Loew are most similar to the pleciofungivorids. It is likely that this hypothesis, which agrees to a certain degree with Hennig's conclusions [9], should, after adding the family Bolitophilidae to the groups noted by Matile, be accepted.

The reconstruction of the way of life of the pleciofungivorids as the prominent bibionomorphs of the Jurassic period is extremely tempting. However, any conclusions about this problem must be expressed with great care, because the pleciofungivorids did not leave direct descendants in the recent fauna, the ecology of which could have been extrapolated to the ancestral forms. Hypotheses concerning the ecology of the larvae have been advanced by Rohdendorf [4] and, in greater detail, by the present author [2, 3]. The imago, judging from the construction of the legs, were good runners. Flight was not distinguished by velocity. The weak development of the mouth parts and the soft labella indicate feeding on liquid nourishment only. Sexual dimorphism in the construction of the antennae, which were longer in the males, suggests that they lived at a significant distance from the females. It is possible that the females possessed stridulating equipment.

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NEW MESOZOIC WATER BEETLES (INSECTA, COLEOPTERA) FROM ASIA

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ABSTRACT: A new species of the family Liadycidae, two new genera and four species of the family Coptoclavidae, a new genus with two new species of the family Dytiscidae, and two new genera and four species of the family Hydrophilidae from the Jurassic and Lower Cretaceous of Central and East Asia are described. Larvae were found together with the imago of three species of Coptoclavidae. These are the first fossil predaceous diving beetles (Dytiscidae) to be described from the Jurassic and Lower Cretaceous deposits.

* * *

Remains of water beetles are found quite often at Mesozoic localities, although by no means as often as one would expect on the basis of their way of life. Several aquatic forms, among which most of the known families of Upper Mesozoic water beetles are represented, are described below.

The stratigraphic position of these finds is of considerable interest, because the geologic age of many insect localities is subject to dispute. The rich fossil remains found at Upper Jurassic localities in Mongolia have not been described, but

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