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Revision of Bibionidae (Diptera) named by Oswald Heer from the Miocene of Öhningen, Southern Germany

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The species of fossil Bibionidae described from the Miocene site of Öhningen, Southern Germany are revised. Three species have been named, but not published, most likely by Oswald Heer, these are formally described here: *Bibio crassinervis* sp. n., *Dilophus pumilio* sp. n. and *Plecia macilenta* sp. n. The genus *Lithosomyia* Carpenter, 1986 (= *Mesomyia* Pongracz, 1928, nec Macquart, 1850) is synonymised with *Bibio* Geoffroy, 1762. *Bibio elongatus* Heer, 1849 is not recognizable to genus and is reclassified as Bibionidae, incertae sedis. *Bibio obsoletus* Heer, 1849 is recognizable as a *Bibio* species but entirely devoid of characters useful for species identification, and is placed as *Bibio*, incertae sedis. *Bibio oblongus* Heer, 1849 is synonymised with *Bibio brevis* Heer, 1849, *Protomyia speciosa* Heer, 1864 is synonymised with *Protomyia amoena* Heer, 1849 and moved to the genus *Penthetria*, and *Protomyia affinis* Heer, 1849 is synonymised with *Plecia jucunda* (Heer, 1849). A key is presented to the recognisable species of Bibionidae from Öhningen. The material from Öhningen consists almost exclusively of female specimens, the problems this raises are discussed.

Keywords: Fossils, Bibionidae, Miocene, Oswald Heer.

INTRODUCTION

Bibionid flies are frequently among the most abundant insects in Tertiary lacustrine fossil deposits. They are known from the Paleocene (Nel 2007), Eocene (e.g., Skartveit 2009), abundantly from the Oligocene (e.g., Théobald 1937, Statz 1943), Miocene (e.g., Heer 1849) and Pliocene (Dürrenfeldt 1968). Thus, the group has a fairly good, rather continuous fossil record from Europe throughout the Tertiary. Bibionids are potentially useful indicators of general climate conditions (Collomb *et al.* 2008), in particular the presence of the warm-climate genus *Plecia* in European Tertiary deposits is evidence of a warmer climate than presently. Unfortunately, the descriptions of numerous species were based on fragmentary material, and many researchers have failed to study previously described material before proceeding to describe new species. This has led to a proliferation of species names in this group, and it is likely that many of these names are synonymous. In addition, cabinet names (or possibly forgotten names, published in publications so obscure that they have been lost for posterity) are common in the collections. Accordingly, there is much need for revisionary work in this group. The first major publication dealing with European fossil bibionids was Oswald Heer's (1849) treatise «Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien» dealing with two Miocene fossil faunas. Since this is the senior work, establishing the identity of Heer's nominal species is an important step towards revising European fossil bibio-

nids. Fortunately, Heer's collections have been preserved largely intact, the Öhningen collection being split between Eidgenössische Technische Hochschule, Zurich (ETHZ) and Staatliches Museum für Naturkunde, Karlsruhe (SMNK), while many of the Radoboj specimens are in Naturhistorisches Museum, Vienna and Landesmuseum Joanneum, Graz. In this paper we illustrate and redescribe the species described from Öhningen by Heer, and also include descriptions of some distinctive taxa that are labeled under cabinet names at the ETHZ.

The late Miocene site of Öhningen is an approximately 13 Myr old calcareous freshwater deposit (Ungricht & Pika-Biolzi, undated). Fossils have been excavated here since the 18th century and the site has yielded a very rich material of fossil animals and plants, roughly 900 species of animals and 500 species of plants have been described from the site to date (Ungricht & Pika-Biolzi, undated). The insect fauna of Öhningen is famous as one of the richest fossil insect faunas known, though it is likely that the number of species names published is an over-estimate of the number of recognisable species from the site (Fikáček & Schmied 2013). The Öhningen insect fossils were mainly described by Heer in four monographs (Heer 1847, 1849, 1853, 1862). Although the descriptions in these monumental works are superior to those of many subsequent treatises of fossil insects, many taxa were described based on very fragmentary material in which few taxonomically useful characters could be observed. Thus the material is in need of revision, and the species should be redescribed and re-illustrated focusing as far as possible on taxonomically relevant characters. The scope of the present paper is to review the available material of bibionid flies from Öhningen, to evaluate, illustrate and redescribe the species named by Heer (1849) and to describe some distinctive taxa that have been named but never published by Oswald Heer.

MATERIAL AND METHODS

This paper is based on material in the Earth Sciences collections of the Swiss Federal Institute of Technology, Zurich (hereafter ETHZ) and Staatliches Museum für Naturkunde, Karlsruhe (hereafter SMNK). The majority of the specimens depicted by Heer (1849) are present in these collections. In many cases, there are more specimens labeled by any particular species name than were mentioned by Heer. Although this is difficult to ascertain, we believe that these additional specimens are from subsequently collected material identified by Heer, who continued to work with fossils for many years after 1849. The exception is a few specimens of *Plecia* at the ETHZ which carry identifications labels by Charles Brongniart (1878). No addition of further specimens after 1878 is apparent from the label data at the ETHZ and in SMNK. Much of the material in ETHZ has no indication of locality in the specimen labels, and to some extent material from Aix-en-Provence (France) and Öhningen appears to be mixed. This problem applies particularly to the specimens labeled with unpublished cabinet names, some of these could possibly originate from Aix-en-Provence. The taxa named under cabinet names were found in drawers where all, or almost all, specimens that could be traced to published records were from Öhningen, thus we believe it is possible but unlikely that some of these may be from Aix-en-Provence, except in the case of some specimens labeled as *Protophila* species, for which a handwritten catalog note states they may possibly be from Aix-en-Provence.

Specimens were photographed using a digital camera (Olympus E3) with a macro lens (Olympus 35 mm f/2.8), this works well since the impressions are flat and two-dimensional. The total length or wing length (whichever was most easily measured) was measured for each specimen, other measurements were taken from the photos using these as standards. Line drawings were produced based on the photos. Scale bars for all drawings = 1 mm. Specimen numbers are given as found in the specimens' labels. As can be expected with fragmentary material, the number of specimens in which measurements could be collected is frequently substantially lower than the total number of specimens, hence the sample size is given for each individual measure, and the measurements given are often not taken from the same specimens. This means that ratios between different measurements cannot be calculated from the data as here presented, since measurements may be from differently-sized specimens.

Morphological terms follow Merz & Haenni (2000), with the following modifications for wing veins (Fig. 9): basal R refers to the section of the first radial vein basad to the furcation with Rs, while the section of this vein distad to the furcation with Rs is referred to as R_1 ; the posterior radial vein is referred to as R_{4+5} both before and after the branching off of R_{2+3} ; basal M refers to the section of the medial vein basad to crossvein R-M, while distal M refers to the section between R-M and the fork in this vein; basal CuA refers to the section of the anterior cubital vein basad to the fork.

RESULTS

Genus *Bibio* Geoffroy, 1762

Syn.: *Mesomyia* Pongracz, 1928, nec Macquart, 1850 (**syn. n.**)
Lithosomyia Carpenter, 1986 (**syn. n.**)

Bibio angustatus Heer, 1849, p. 215–216

(Figs 1–4)

Material. Lectotype (herein designated) female labeled Oe. 179 Inv. 1274 (SMNK, Fig. 1). — Paralectotypes: (herein designated) 3 females (Oe. 151–153, SMNK, Fig. 2), 5 females (lot Pl. I 851, ETHZ). The lectotype is the specimen depicted by Heer (Pl. XVI Fig. 4).

Diagnosis. A rather large species with body length 13–14 mm in females, apparently brachypterous with wing short and broad, approximately 7 mm long. Body and legs black, wing blackish fumose with distinctive venation and dark pterostigma. The species is habitually similar to *Bibio elongatus* (for the characters that can be observed in the latter species) but can be recognized by its smaller size (13 vs. 18 mm).

Redescription. All specimens at hand are 13–14 mm long except for SMNK Oe. 153 which is 11 mm but with the abdominal tip missing. The species appears to have been entirely black, the wings are also blackish fumose.

Head: not well preserved in any of the specimens. Antennal flagellum apparently short and stout, segments not possible to count.

Thorax: black. Length 2.9–3.7 mm (N = 2).



Fig. 1. *Bibio angustatus*, ♀, lectotype. SMNK Oe. 179.



Fig. 2. *Bibio angustatus*, ♀, paralectotype. ETHZ Pl. I 851.

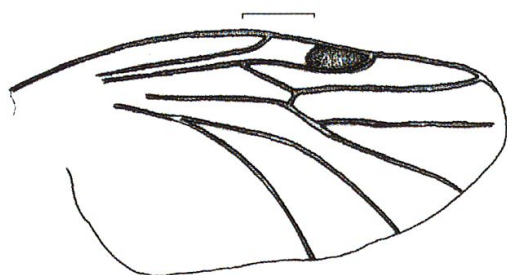


Fig. 3. *Bibio angustatus*, ♀, wing. SMNK Oe. 179.

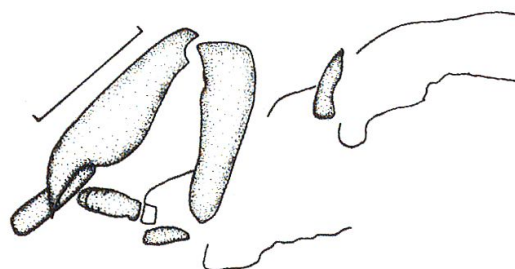


Fig. 4 *Bibio angustatus*, ♀, head, thorax and foreleg. ETHZ Pl. I 851.

Wing (Fig. 3): Length 6.8–7.0 mm (N = 3), width 3.6 mm (N = 2) length/width 1.9–2.0 (N = 2). Blackish fumose, veins distinctive and brown, pterostigma blackish, R-M less than half as long as Rs. Costa distinctively curved. CuA₁ thicker than the other veins, prominent. Vein measurements: Basal R 2.5–2.9 mm (N = 2), Rs 0.6–0.9 mm (N = 2), R₁ 1.7 mm (N = 1), R-M 0.3 mm (N = 2), R₄₊₅ 2.3–3.4 mm (N = 2), basal M 2.4 mm (N = 1), distal M 0.4 mm (N = 1), M₁ 3.2 mm (N = 1), M₂ 2.8 mm (N = 1), CuA₁ 2.9 mm (N = 1).

Legs (Fig. 4): Protibia 1.6–1.8 mm long (N = 2) by 0.6 mm wide (N = 1), relatively thick, hind leg comparatively short and slender, with femur and tibia 2.3 mm long (both N = 1). Tarsi slender.

Abdomen: Length 9.1–9.6 mm (N = 2).

Discussion. Heer (1849) mentioned four specimens from the «Carlsruhe collection» in his original description, and there are still four specimens labeled as this species in SMNK. They are all weak impressions of female *Bibio*. The best pre-

served of these specimens has a body length of 14 mm, but the wing is just 7 mm long, suggesting that the species had brachypterous (and almost certainly flightless) females. In recent Diptera, brachyptery is often more pronounced in, or limited to, females. Thus, the male of this species may have had normally developed wings. The abdomen of the best preserved specimens does not appear to be conspicuously bloated, thus we believe that the apparent brachyptery in this species is real and not a taphonomical artifact. The wing is short and broad, has a distinctively curved Costa and the placement of the wing veins appears to be somewhat unusual, for instance CuA_1 and CuA_2 appear to run unusually close together, and the apical part of M_2 looks wavy. While some of this may be due to post mortem deformation, deviations in wing venation are commonly seen in brachypterous specimens. Since the specimen with the most visible venation is very heavily pigmented and the thorax appears to have been strongly sclerotized, it is unlikely to be a teneral specimen with not-yet-expanded wings. Of the nine specimens classified as this species, only two are reasonably well preserved with some recognisable characters available. Of these, the lectotype seems to have hyaline wings while those of one of the Zurich specimens are blackish fumose. However, the lectotype shows generally poor preservation of colour and it is quite plausible that the wings may originally have been much darker.

***Bibio brevis* Heer, 1849, p. 225–226.**

(Figs 5–16)

Synonym: *Bibio oblongus* Heer, 1849, 227. **Syn. n.**

Material. Lectotype (herein designated) female ETHZ Pl. I 856 (recognizable from Fig. 5). — Paralectotypes: 1 female (ETHZ, Coll. Lavater), 14 females (ETHZ Pl. I 856, Fig. 6), 1 female (SMNK Oe 160, Inv. 1193). — Additional material: Lectotype (female) of *Bibio oblongus* (ETHZ, labeled with reference to Heer's illustration Pl. XVI Fig. 18). 1 female (ETHZ, ex coll. Lavater), 1 female (ETHZ lot Pl. I 859), 1 female (SMNK Oe. 156). All of these labeled as *Bibio oblongus* Heer. — Uncertain affinity: male (ETHZ lot Pl. I 865, Fig. 7) identified as *Bibio brevis*, male (ETHZ Pl. I 887, Fig. 8) labeled with the cabinet name *Bibio infernalis*.

Diagnosis. A medium-sized, rather stocky *Bibio* species. Total length of the specimens measured 7.5–9.5 mm, wing length 6.0–7.6 mm. Of the other species described from Öhningen it differs from *Bibio elongatus* and *Bibio angustatus* by the much smaller size, from *Bibio pulchellus* by the considerably more robust body. *Bibio moestus* is much darker coloured, with an all-black body and blackened wings. The species is rather similar to *Bibio fusiformis* but seems to differ in having dark anterior wing veins and a well-defined pterostigma, as well as being a bit smaller. The male (tentatively associated) has hyaline wings with black pterostigma, radial sector 2.8–4 times as long as R-M, epandrium with a wide mesal cleft.

Redescription. Female (Figs 5–6, 9–13):

Head: not well preserved in any of the specimens at hand, but appears to be black (like in almost all known Bibionidae). Antenna not well preserved in any of the specimens.

Thorax brownish-black, 2.4 mm long and 2.0–2.1 mm wide (N = 2). Haltere brown.



Fig. 5. *Bibio brevis*, ♀, lectotype. ETHZ, labelled Taf. XVI Fig. 16a.

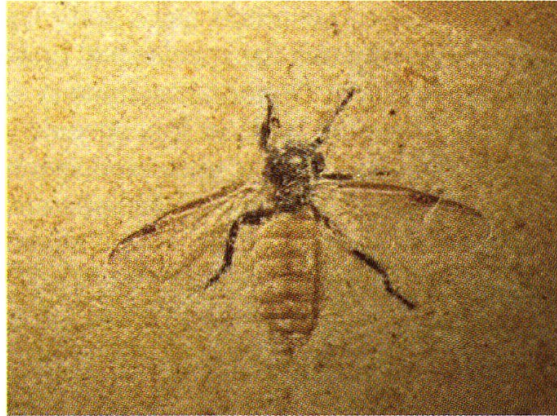


Fig. 6. *Bibio brevis*, ♀, paralectotype. ETHZ Pl. I 856.



Fig. 7. *Bibio* ?*brevis*, ♂. ETHZ Pl. I 865.



Fig. 8. *Bibio* ?*brevis*, ♂. ETHZ Pl. I 887.

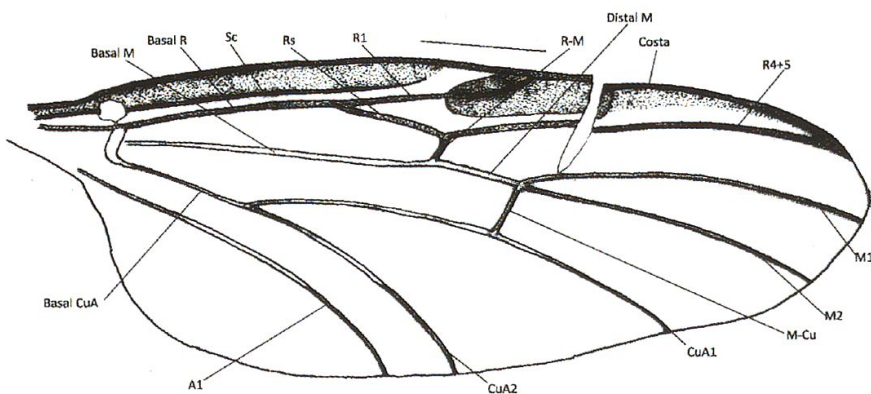


Fig. 9. *Bibio brevis*, ♀, wing. ETHZ Pl. I 856.

Wing (Fig. 9): Length 6.1–7.3 mm (N = 4), width 2.5–3.0 mm (N = 3), length/width = 2.3–2.7 (N = 6, includes specimens for which absolute wing length was not measured). Apparently hyaline with darkened anterior edge (anterior half of area anterior to R₁ proximally and to R₄₊₅ distally) and a well-defined, dark brown pterostigma. Costa extends slightly beyond apex of R₄₊₅. Humeral vein not visible, Subcosta fine but distinctive. Crossvein R-M approximately half as long as basal

part of Rs. M and CuA-veins apparently colourless. Crossvein M-Cu meets M_1 some distance distal to fork of M. Length of vein segments ($N = 1$) Sc 3.3 mm, Basal R 2.8 mm, R_1 1.5 mm, Rs 0.9 mm, R_{4+5} 2.7 mm, R-M 0.3 mm, Basal M 2.5 mm, distal M 0.9 mm, M_1 approx. 2.7 mm, CuA_1 approx. 3.2 mm.

Legs (Figs 10–12): brownish-black, moderately robust. Front tibia 1.6 mm long ($N = 1$), spur of front tibia a little less than half the length of apical spine, first tarsomere 1.1 mm long ($N = 1$). Hind femur clavate, hind tibia relatively slender for the genus, 2.1–2.2 mm long ($N = 2$), hind tarsus not thickened. Pile not possible to see in the specimens available.

Abdomen (Fig. 13): 5.6–5.8 mm long ($N = 2$), 2.2–2.4 mm wide ($N = 2$), yellowish-brown to dark brown (uncertain if the observed variation is due to individual variation or taphonomy). Three spermathecae are visible in some of the specimens. Cerci rather small, apparently somewhat pointed.

Male (tentatively associated, Figs 7–8, 14–16):

Head: Black, length 1.0 mm ($N = 1$). The antennal flagellum is rather slender and 6- or 7-segmented (distal part not well preserved).

Thorax: Length approximately 2.0 mm ($N = 1$). Black. Not well preserved in any of the specimens available.

Wing (Fig. 14): Length 6.0–7.0 mm ($N = 2$), width 3.0 mm ($N = 1$), length/width = 2.4 ($N = 1$). Hyaline with a very distinctive, black pterostigma. R-veins pale brown, posterior veins colourless. Wing venation as in female. Radial sector 2.8–4 times as long as R-M. Measurements: Sc 2.9–3.9 mm ($N = 2$), Basal R 2.4 mm ($N = 2$), R_1 1.7–2.2 mm ($N = 2$), Rs 0.5–0.7 mm ($N = 2$), R_{4+5} 3.0–3.3 mm ($N = 2$), R-M 0.17–0.18 mm ($N = 2$), basal M 2.2 mm ($N = 1$), distal M 0.7 mm ($N = 1$), M_1 2.6 mm ($N = 1$), M_2 2.4 mm ($N = 1$), M-Cu 0.7 mm ($N = 1$), basal CuA 0.9 mm ($N = 1$), CuA_1 3.0 mm ($N = 1$), CuA_2 2.5 mm ($N = 1$).

Legs (Fig. 16): Black. Fore tibia of the usual shape for the genus, length of tibial spur not possible to estimate. Length of fore tibia 1.5 mm ($N = 1$), fore first tarsomere 0.8 mm ($N = 1$), hind femur 2.5 mm ($N = 1$), hind tibia 2.5 mm ($N = 1$), hind first tarsomere 1.0 mm ($N = 1$). Hind leg relatively slender, tarsus not thickened.

Abdomen: Length 5.3 mm ($N = 1$). Black. Terminalia (Fig. 15) with sickle-shaped gonostyli as usual for the genus *Bibio*, the epandrium is rather small with a wide, V-shaped cleft between the two lateral lobes.

Discussion. Heer (1849) mentioned six female specimens in the original description, one from Karlsruhe, four from Coll. Lavater and one from Coll. Seyfried. In all likelihood, the five latter are among the ones labeled as *Bibio brevis* in ETHZ. Though Heer's figures (Pl. XVI, Figs 16a and 16b) are sparse in detail, the specimens in Karlsruhe must be the original for Fig. 16a and one of the ETHZ specimens the original for Fig. 16b. Surprisingly, these specimens are among the least well-preserved of those available.

The nominal species *Bibio oblongus* was described from two specimens in coll. Lavater. In ETHZ there is one specimen labeled Pl. XVI Fig. 18 (correctly), one very faint impression labeled «Coll. Lavater» which is probably the one depicted by Heer Fig. 18c, and one specimen (Pl. I 859) not depicted by Heer. In SMNK one specimen (Oe. 156) which is a very weak impression. These specimens cannot be distinguished from specimens identified as *Bibio brevis* and the name should be regarded as a synonym of *Bibio brevis*.

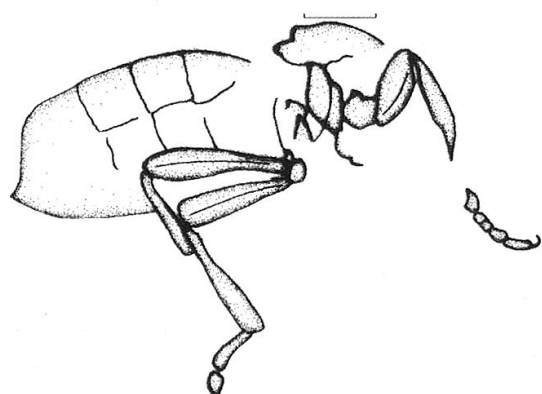


Fig. 10. *Bibio brevis*, ♀, body and legs. ETHZ Pl. I 856.

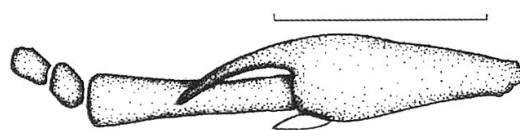


Fig. 11. *Bibio brevis*, ♀, fore leg. ETHZ Pl. I 856.

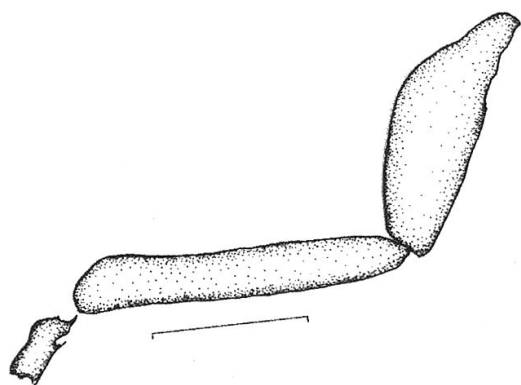


Fig. 12. *Bibio brevis*, ♀, hind leg. ETHZ Pl. I 856.

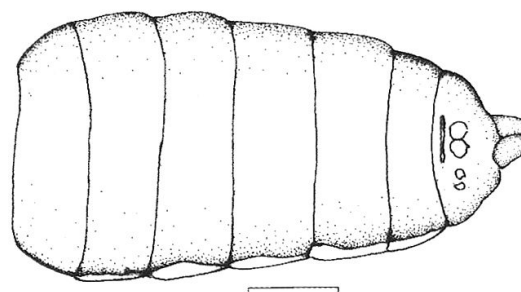


Fig. 13. *Bibio brevis*, ♀, abdomen, dorsal view. ETHZ Pl. I 856.

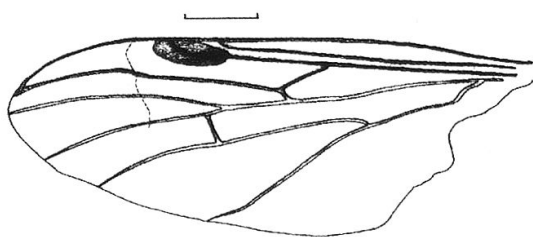


Fig. 14. *Bibio ?brevis*, ♂, wing. ETHZ Pl. I 865.

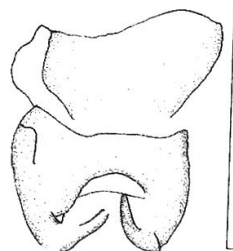


Fig. 15. *Bibio ?brevis*, ♂, terminalia. ETHZ Pl. I 887.

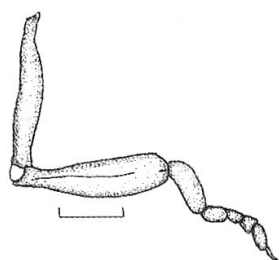


Fig. 16. *Bibio ?brevis*, ♂, hind leg. ETHZ Pl. I 887.

The male labeled as a possible male of *Bibio brevis* is probably conspecific with a male labeled with the cabinet name *Bibio infernalis*. The association of these specimens with the females described as *Bibio brevis* is hypothetical, based mainly on similar size and both having a short R-M vein. The wing colour is strikingly different in the two groups, however *Bibio* females often have much darker wings than conspecific males, e.g. in the recent *Bibio hortulanus* and *B. leucopterus*. There is a second specimen at the ETHZ labeled as *Bibio infernalis* (Pl. I 887). This specimen is recognisable as a *Dilophus* female, possibly conspecific with *Dilophus pumilio* but devoid of taxonomically useful characters.

This species was placed in the new genus *Mesomyia* by Pongracz (1928). The genus is supposed to differ from *Bibio* in having elliptical, as opposed to subtriangular, wings as well as numerous crossveins in the middle on the wing. Pongracz described *Mesomyia* from a specimen from Radoboj, Croatia which he identified as *Bibio brevis* Heer from Heer's description. He did not study type material of this species and in his treatment of fossil bibionids commented that he found Heer's drawings lacking in clarity (Pongracz 1928 p. 174), yet had no hesitation to identify his specimen with a species described by Heer from a different site, despite noting several differences between the original description and the specimen at hand.

Pongracz (1928) drew the wing of this species with numerous crossveins between veins R_{4+5} , M , M_1 and CuA_1 . These «veins» were believed by Pongracz to demonstrate that the species had retained a primitive wing venation with numerous crossveins, accordingly he reclassified it in a new genus *Mesomyia*. As this name was previously used by Macquart (1850), the genus was renamed *Lithosomyia* by Carpenter (1986). However, when examining the specimens in ETHZ we could find no trace of the crossveins drawn by Pongracz, on the contrary the wing venation was typical of the genus *Bibio*. Confusingly, Pongracz based his reclassification on a specimen from Radoboj, Croatia in the Natural History Museum, London whereas Heer (1849: 225) only mentioned specimens from Öhningen in the original description – the specimen studied by Pongracz thus cannot be from the type series. The presence of this species from Radoboj has not been indicated by other authors than Pongracz.

***Bibio crassinervis* sp. n.**

(Figs 17–21)

Material. Holotype female (ETHZ lot Pl. I 851, Fig. 17). — Paratypes: 5 females (ETHZ lots. Pl. I 851 (2), Pl. I 862, Pl. I 875, Pl. I 888, Fig. 18).

Etymology. Name presumably given by Heer. From Latin *crassus*, thick and *nervus*, sinew, referring to the unusually thick wing veins on this species.

Diagnosis. A large *Bibio* with narrow wings (2.5–2.8 times as long as wide) with very strong, dark veins, black, oval pterostigma. The head and mesonotum are black, thorax laterally with yellowish-brown patches on meron, abdomen yellowish-brown. The legs are yellowish-brown with narrowly black tips on the femorae, tibiae and innermost two tarsomeres, the outer tarsomeres black. The protibia is rather stout with an unusually short outer spine extending less than one-fourth the length of the first tarsomere. The wings are light brownish fumose, with dark brown veins and black pterostigma.

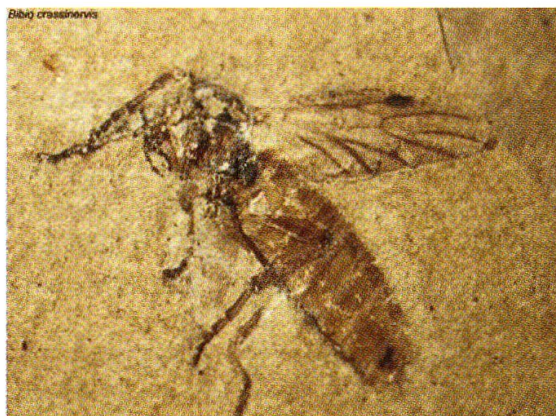


Fig. 17. *Bibio crassinervis*, ♀, holotype. ETHZ Pl. I 851.



Fig. 18. *Bibio crassinervis*, ♀, paratype. ETHZ Pl. I 851.

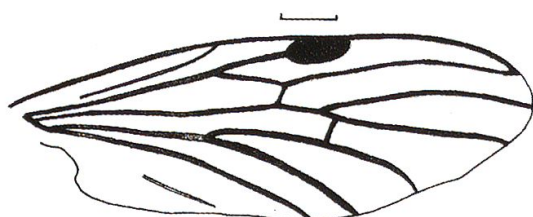


Fig. 19. *Bibio crassinervis*, ♀, wing. ETHZ Pl. I 851.

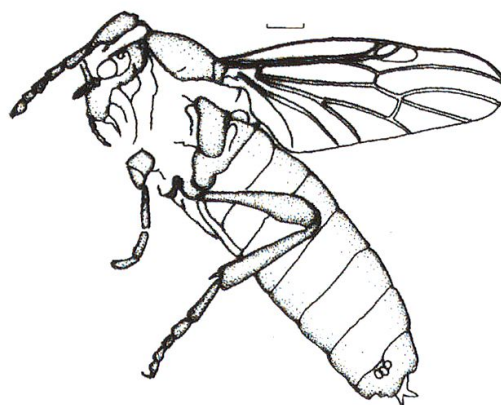


Fig. 20. *Bibio crassinervis*, ♀, body. ETHZ Pl. I 851.

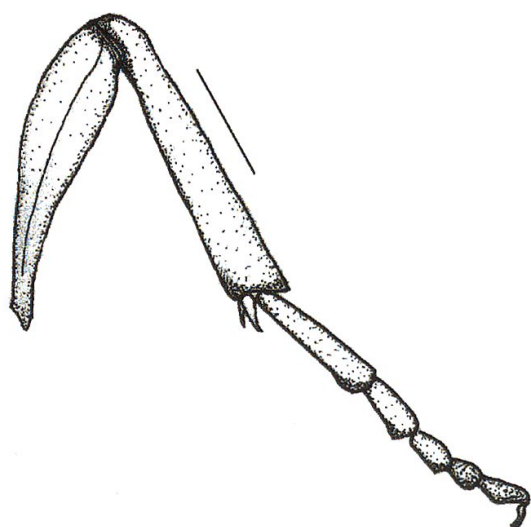


Fig. 21. *Bibio crassinervis*, ♀, hind leg. ETHZ Pl. I 851.

Description. Female: Habitus as in Fig. 20. Body length 11–13 mm (N = 6).

Head: Length 1.6–2.1 mm (N = 2). Black. Antenna short and relatively slender, segments not possible to count (flagellum possibly six-segmented). Palp relatively long.

Thorax: rather crushed and deformed in the specimens at hand, but mesonotum and scutellum appear to be black, humeri and parts of pleurae (at least meron) yellowish-brown. Pile not visible in any of the specimens.

Wing (Fig. 19): Length 7.5–8.5 mm (N = 4), width 3.0–3.4 mm (N = 3), length/width = 2.5–2.7 (N = 4). Rather slender, apparently light brown fumose. Veins particularly strong and prominent, most so in the apical half of wing. Pterostigma oval, black, highly distinctive. Humeral vein absent, Subcosta distinctive. Crossvein R-M a little less than half as long as Rs. Fork of CuA rather short, not much longer than stem. M-Cu meets M_1 slightly beyond fork of M. A_1 distinctive, straight. Measurements (N = 4): Basal R 2.7–3.3 mm, R_1 1.9–2.8 mm, Rs 0.9–1.1 mm, R_{4+5} 3.2–4.1 mm, R-M 0.3–0.5 mm, basal M 2.6–3.5 mm, distal M 0.7–1.0 mm, M_1 2.5–4.3 mm, M_2 2.1–3.1 mm, M-Cu 0.4–0.7 mm, basal CuA 1.6–2.6 mm, CuA_1 3.3–4.6 mm, CuA_2 2.1–2.8 mm, A_1 2.6–4.0 mm.

Legs (Fig. 21): Yellowish-brown with the apices of femorae, tibiae and the innermost two tarsal segments narrowly black, the outermost three tarsal segments black. Protibia rather stout, tibial spur apparently less than half as long as spine. Hind femur moderately clavate, hind tibia slender, apically truncate, hind first tarsomere slender.

Abdomen: Uniformly yellowish-brown. Three spermathecae visible in one of the specimens.

Discussion. There are seven female specimens of a highly distinctive *Bibio* species labeled under the name *Bibio crassinervis* at the ETHZ, apparently from Öhningen. The name was probably given by Heer but appears never to have been published (Ungricht, personal communication). We believe the name to be a cabinet name of Heer's as we have not been able to trace it to any publication. The distinctive wing venation is shared with *Bibio curtisii* Heer, 1856 from Aix-en-Provence, except that the latter species has got humeral vein between Sc and C, approximately at the level of the basal vein. *Bibio curtisii* was described from males but there are also female specimens in the material (labeled by the cabinet name *Bibio martinsi*) which have a humeral vein but are otherwise fairly similar to *Bibio crassinervis*.

***Bibio elongatus* Heer, 1849, 214**

(Figs 22–23)

Material. Holotype (female) SMNK (Oe. 154 Inv. 1189, Fig. 22). — Additional material, tentatively associated: ETHZ (S.N. 189 Pl. I 863), ?male, just legs and wings discernible.

Diagnosis. A large, slender species, body length approximately 18 mm. The female appears to be brachypterous, with a wing length of 9 mm, wing width 3.7 mm. No trace of legs or antennae in the specimen, details of head and thorax not possible to see, as for most details of the wing venation (Fig. 23). The head is 1.5 mm long, thorax 3.9 mm long by 2.7 mm wide. The impression is of an uniform, brownish colour.



Fig. 22. *Bibio elongatus*, ♀, holotype. SMNK Oe. 154.

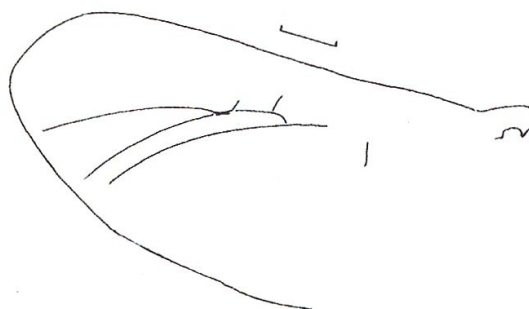


Fig. 23. *Bibio elongatus*, ♀, wing. SMNK Oe. 154.



Fig. 24. *Bibio fusiformis*, ♀, lectotype. ETHZ Taf. XVI Fig. 4c.



Fig. 25. *Bibio fusiformis*, ♀, paralectotype. ETHZ Pl. I 858.

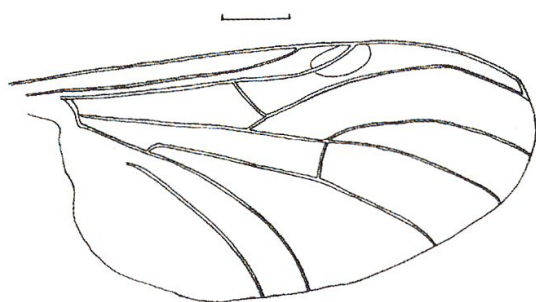


Fig. 26. *Bibio fusiformis*, ♀, wing. ETHZ Pl. I 858.

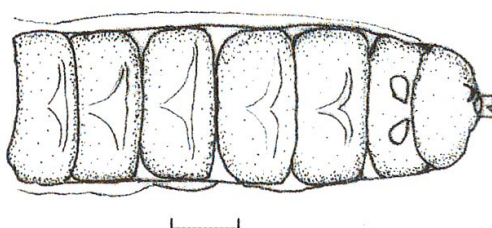


Fig. 27. *Bibio fusiformis*, ♀, abdomen. ETHZ Pl. I 858.

Discussion. The specimen depicted by Heer (1849) is in SMNK (Oe. 154 Inv. 1189). As Heer (1849) mentioned only one specimen in his description, this should be regarded as the holotype. It is a female specimen, 18 mm long, unfortunately rather poorly preserved and devoid of recognizable characters. There is one *Bibio* specimen (presumably male) which has been identified as this species, presumably by Heer, in ETHZ (S.N. 189, Pl. I 863). The specimen has the first two pairs of legs

and the wings reasonably well preserved, other parts scarcely discernible. With a wing length of 13.5 mm the large size would suggest that it could be conspecific with the female in Karlsruhe, but this is highly uncertain. The wings are much narrower than in the female (length/width = 3.1 vs. 2.4 in the female), on the other hand brachypterous specimens often have relatively broader wings. The Zurich specimen is habitually very different from the Karlsruhe specimen, and it is not at all clear why they have been identified as the same species.

Apparent brachyptery in fossils should be treated with some caution, as partial decomposition before fossilization is likely to lead to stretching of the abdomen, thus increasing the apparent length of the specimen. If just the length of the abdominal tergites are measured, the body length decreases to approximately 16 mm, still very long for a specimen with 9 mm wings. The specimen is a very weak impression, the only recognizable traits is its large size and apparent brachyptery. Even the genus placement is uncertain – the wing shows traces of what may possibly be a vein R_{2+3} , and the crossvein R-M may be vertical, in which case the species should be placed in *Plecia* and not in *Bibio*. Since neither legs nor the anterior part of the wing are preserved, the species should be regarded as Bibionidae, incertae sedis.

***Bibio fusiformis* Heer, 1849, 219**

(Figs 24–29)

Material. Lectotype (female, herein designated) ETHZ . Labeled: Heer Pl. XVI Fig. 4 [sic!] c (fig. 24). — Paralectotypes (13 females, Fig. 25) ETHZ two females (Pl I 858), two females (Pl. I 861) SMNK 9 females (Oe. 142–145, Oe. 148, Oe 161 – two specimens, Oe. 194). Additional material (1 male, tentatively associated) ETHZ Pl. I 861.

Diagnosis. A medium-large *Bibio* species, body length 9.5–12 mm. Head and thorax apparently black, legs and abdomen brown. Wing quite broad, length/width = 2.2–2.6, hyaline with light brown veins, pterostigma light brown. Vein R-M rather short, approximately one third the length of Rs. Further details are not possible to see in the specimens at hand. It can be distinguished from *Bibio brevis* females by the larger size and the hyaline wings.

Redescription. Female

Habitus as in Figs 24–25. Total length 9.5–12.3 mm (N = 8).

Head: not possible to see well in any of the specimens at hand.

Thorax: Length 2.9–3.4 mm (N = 3). Blackish-brown.

Legs: Blackish-brown. Length of hind femur 2.5 mm (N = 2), hind tibia 2.6–2.7 mm (N = 2).

Wing (Fig. 26): Length 7.3–10.1 mm (N = 7), width 2.9–4.0 mm (N = 6), length/width = 2.2–2.6 (N = 5). Apparently hyaline with light brown veins. Humeral vein absent, Subcosta relatively strong. Pterostigma distinctive. Basal part of Rs rather steep, 1.8–3.0 times as long as R-M (N = 4). R_{4+5} distally strongly curved, costa extends to apex of R_{4+5} . Crossvein M-Cu meets M at fork. Vein measurements: Basal R 2.6–2.9 mm (N = 3), R_1 1.9–2.4 mm (N = 3), Rs 0.7–1.0 mm (N = 3), R-M 0.25–0.40 mm (N = 3), R_{4+5} 3.3 mm (N = 1), basal M 2.5–2.6 mm (N = 2), distal M 0.5–0.9 mm (N = 2), M_1 3.2 mm (N = 1), M_2 2.7 mm (N = 1), M-Cu 0.5 mm (N = 1), Basal CuA 1.5 mm (N = 1), CuA₁ 3.9 mm (N = 1), CuA₂ 2.4 mm (N = 1).



Fig. 28. *Bibio ?fusiformis*, ♂.



Fig. 29. *Bibio ?fusiformis*, ♂, body. ETHZ Pl. I 861.



Fig. 30. *Bibio moestus*, ♀, lectotype. ETHZ Pl. I 857.



Fig. 31. *Bibio moestus*, ♀, paralectotype. SMNK Oe. 157.

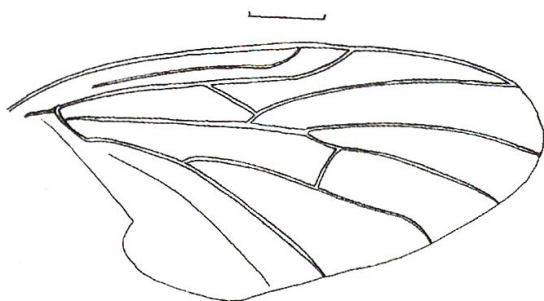


Fig. 32. *Bibio moestus*, ♀, wing. ETHZ Pl. I 857.



Fig. 33. *Bibio moestus*, ♀, forebody. SMNK Oe. 157.

Abdomen (Fig. 27): Length 6.1–8.8 mm (N = 5), yellowish-brown.

Male (tentatively associated, Figs 28–29)

A single specimen in ETHZ, reasonably preserved lying with the ventral side up. The specimen agrees well with the females of *B. fusiformis* in size and wing venation, except that M and CuA have much longer stems and shorter forks.

Total length 10.5 mm. N = 1 for all measurements and ratios.

Head: Head width 1.3 mm. Antenna rather slender, flagellum probably six- or seven-segmented.

Thorax: Length 2.5 mm. Only outline preserved.

Wing: Length 7.0 mm, width 2.8 mm, length/width = 2.5. Hyaline with light brown veins, pterostigma just discernible. Basal part of Rs 2.2 times as long as R-M. R_{4+5} distally somewhat curved, Costa extends to apex of R_{4+5} . Crossvein M-Cu meets M_1 slightly beyond fork of M. A_1 distinctive, straight. Vein measurements: Basal R 2.8 mm, R_1 1.4 mm, Rs 0.8 mm, R-M 0.35 mm, R_{4+5} 3.0 mm, basal M 3.2 mm, distal M 1.0 mm, M_1 2.2 mm, M_2 1.9 mm, M-Cu 0.24 mm, Basal CuA 3.3 mm, CuA_1 1.8 mm, CuA_2 1.5 mm.

Legs: No pigmentation preserved in specimen except that tip of hind femur appears to be darkened. Hind tibia 2.8 mm long, 0.47 mm wide. Hind tarsus slender.

Abdomen: Brown. Length 7.2 mm, width 2.3 mm. Sternite VIII with a relatively shallow, V-shaped indentation. Gonostyles sickle-shaped as usual for genus.

Discussion. Heer (1849) mentioned nine specimens, two from coll. Seyfried, one from coll. Lavater and six from Karlsruhe. One specimen in ETHZ is the one depicted by Heer (Pl. XVI Fig. 9c). The outline of this specimen appears to be enhanced by pencil and it is thus difficult to interpret as the original borders of the structures are not possible to see, at least in the wing the pencil enhancement misses the veins it was meant to enhance considerably. Two further female specimens in ETHZ (Pl. I 858) are reasonably well preserved but do not fit any of Heer's figures. Of a lot of six specimens (Pl. I 861) labelled as *B. fusiformis* one male and two females show sufficient characters to be recognisable. There are nine specimens in the SMNK collection of which the two specimens both labeled as Oe. 161 are the ones depicted in Pl. XVI Figs 9a, 9b. One specimens in SMNK (Oe. 147) labeled as *Bibio fusiformis* has a short vein R_{2+3} and thus belongs in the genus *Plecia*. All the other specimens are relatively faint impressions of medium-sized female *Bibio*, a fact also noted by Heer (1849). The species appears to be quite similar to *Bibio brevis*, differing only in being somewhat larger. The preservation of these specimens is somewhat different from the *B. brevis* specimens, most appear as relief impressions with few or no traces of organic matter.

In Naturhistorisches Museum, Vienna there is a specimen labeled as «*Bibio fusciformis* Heer» from Radoboj, Croatia. This specimen is, however, a *Penthetria* female and the species has not been found in Radoboj.

***Bibio moestus* Heer, 1849, 224–225.**

(Figs 30–33)

Material. Lectotype (female) SMNK Oe. 163. This is the specimen depicted by Heer (Pl. XVI Fig. 15c). — Paralectotypes: ETHZ Pl. I 855 – female – labeled with cabinet name *Bibio spectabilis* (nec *Bibio spectabilis* Théobald, 1937); ETHZ

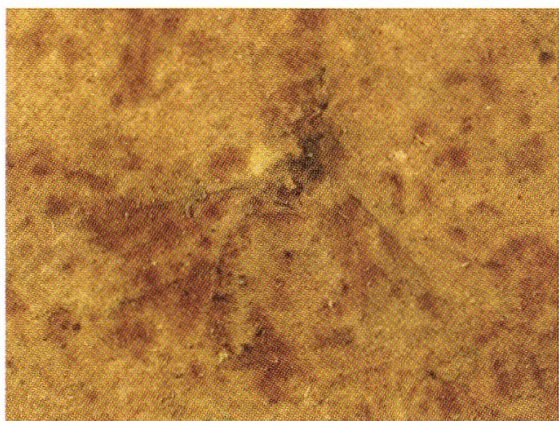


Fig. 34. *Bibio obsoletus*, ♀, holotype. SMNK Oe. 161.



Fig. 35. *Bibio pulchellus*, ♀, lectotype. ETHZ Pl. I 854.

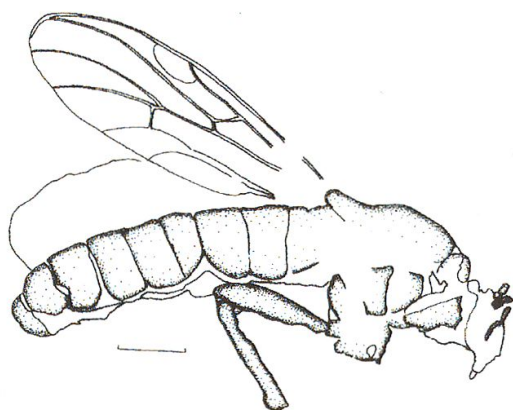


Fig. 36. *Bibio pulchellus*, ♀, body. ETHZ Pl. I 854.



Fig. 37. *Bibio* ?*pulchellus*, ♂. ETHZ Pl. I 854.



Fig. 38. *Dilophus pumilio*, female, holotype. ETHZ Pl. I 886.

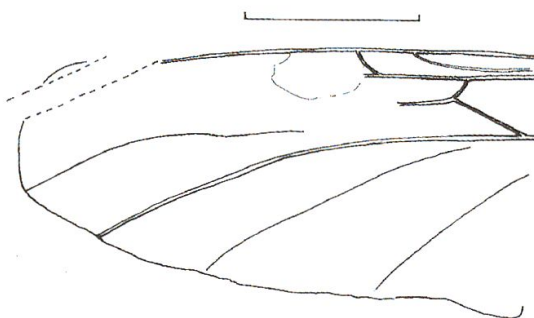


Fig. 39. *Dilophus pumilio*, female, wing. ETHZ Pl. I 886.

Pl. I 857 – two females; SMNK Oe. 157 – female – could possibly be the counterpart of that depicted in Heer (1849)'s Fig. 15b – Heer's figure indicates an obvious crack in the rock that is not found in this specimen. Heer (1849) mentioned two specimens from Coll. Lavater, one from coll. Seyfried, one from coll. Fürstenberg and four from Karlsruhe.

Diagnosis. A moderately large *Bibio* species (body length 10–11 mm), entirely black with dark fumose wings. Wing rather wide, 2.2 times as long as wide. Basal radial sector two to three times as long as R-M. The ETHZ specimens suggest this was an all-black species with blackish wings, habitually similar to the recent *Bibio leucopterus*.

Redescription. Female: Habitus as in Fig. 33. Total length 10–11 mm (N = 4) Head, body and legs entirely black, wing dark blackish fumose.

Head: No details discernible in head or antenna. Distal segment of palp cylindrical.

Thorax: Length 2.7–3.3 mm (N = 4). Entirely black. Haltere dark brownish.

Wing (Fig. 32): Length 6.5–8.4 mm (N = 5). Width 3.0–3.3 mm (N = 3), length/width = 2.2 (N = 3). Blackish brown fumose, veins distinctive, no discernible humeral crossvein between Sc and Costa. Area anterior to R-veins darker than more posterior area, pterostigma indistinctive. Radial sector two to three times as long as R-M. Crossvein M-Cu meets M_1 a little distal to fork of M. A_1 distinctive, straight. Vein measurements: Basal R 2.3–2.6 mm (N = 3), R_1 1.6–1.8 mm (N = 2), R_s 0.66–0.81 mm (N = 3), R-M 0.24–0.29 mm (N = 3), R_{4+5} 2.9–3.8 mm (N = 3), basal M 2.1–2.5 mm (N = 3), distal M 0.6–0.9 mm (N = 3), M_1 2.6–3.1 mm (N = 3), M_2 2.3–2.5 mm (N = 3), M-Cu 0.4–0.5 mm (N = 2), Basal CuA 1.9 mm (N = 1), CuA_1 3.1 mm (N = 1), CuA_2 2.3 mm (N = 1).

Abdomen: Length 7.4–8.2 mm (N = 3). Entirely black. Cerci small and pointed.

Legs: Entirely black. Femorae moderately thickened, tibiae and tarsi slender. Measurements: fore femur 1.6–1.9 mm long (N = 2), 0.5–0.7 mm wide (N = 2), fore tibia 1.5–1.7 mm long (N = 3), first fore tarsomere 1.0–1.2 mm (N = 2), hind femur 2.4–2.7 mm long (N = 2), 0.65–0.67 mm wide (N = 2), hind tibia 2.3–2.5 mm long (N = 3), 0.3–0.4 mm wide (N = 2), first hind tarsomere 0.8–0.9 mm (N = 2). Spur of hind tibia long and slender.

Discussion. Heer (1849) described this species as having hyaline wings. However, the two specimens in SMNK that probably were illustrated by Heer show no trace of pigment in the wings at all, hence the wing colour is unknown. The dark-winged specimens in ETHZ are similar to the SMNK specimens in size, wing venation and in the shape and colour of the legs. In ETHZ there is one female (labeled S.N. 160) labelled as *B. moestus*, which differs from the others in having hyaline wings with dark veins and a dark pterostigma. Given the colour of the veins and pterostigma the wing colour is most likely preserved in this specimen, hence it is probably a different species from the dark-winged ones in ETHZ. It is not clear where this specimen originates from, it could possibly be the specimen from Aix-en-Provence mentioned by Heer (1856: 33–34), which was said to have a striking black stigma. This is not apparent in any of the two specimens from SMNK illustrated by Heer, nor in Heer's own illustrations (Pl. XVI Fig. 15, 15b, 15c).

***Bibio obsoletus* Heer, 1849, 227–228.**

(Fig. 34)

Material. Lectotype (herein designated) (female) SMNK Oe. 161 – this is the specimen depicted by Heer (Pl. XVI Fig. 19, 19a).

Discussion. Described from a specimen in the Karlsruhe collection. One very weak impression in SMNK (Oe. 161). This specimen is a 7 mm long female specimen entirely devoid of recognizable characters. The basal parts of the wings are fairly visible showing that the basal section of Rs is markedly longer than the oblique R-M, confirming the specimen as a *Bibio*. It should be regarded as *Bibio*, incertae sedis.

In Naturhistorisches Museum, Vienna there is a specimen from Radoboj, Croatia identified as *Bibio obsoletus*. This specimen, which has fairly well preserved wings, is labeled as having been acquired in 1884. There is no indication of this specimen having been identified by Heer (who died in 1883) and its association with the species from Öhningen is highly uncertain. There is also a specimen from Corent, France illustrated (Oustalet 1870, Pl. 4, Fig. 13) and described by Oustalet (1870), which was tentatively identified as this species. This specimen, currently in Muséum National d'Histoire Naturelle, Paris, is entirely devoid of taxonomically useful characters but vaguely recognisable as a bibionid female.

There is one male specimen in ETHZ (Pl. I 860) labeled as this species. Just the inner part of the wings are exposed in this specimen, but it shows a vertical R-M crossvein. The specimen also has a slender protibia, which, together with its slender body, small head and coal-black colour identifies it as belonging to the genus *Penthetria*.

***Bibio pinguis oeningensis* Heer, 1849, 221**

The subspecies was described from a specimen in the collection of the Rheinau monastery, we have not seen this specimen. There is a syntype of *Bibio pinguis* from Radoboj in the Museum of Natural History, Vienna, which is the specimen described as «var. Paulo minor» and depicted by Heer (Pl. XVI Fig. 11 c).

***Bibio pulchellus* Heer, 1849, 217**

(Figs 35–36)

Material. Lectotype (herein designated, female) ETHZ Pl. I 854 (specimen depicted in Fig. 35). — Paralectotypes: 1 male, 1 female, ETHZ Pl. I 854.

Heer (1849) described this species from a specimen in the Seyfried collection. There are three specimens (Pl. I 854) in ETHZ labeled as this species, but none of them are the specimen depicted by Heer (Pl. XVI Fig. 6).

Diagnosis. A medium-sized *Bibio* with body length 7.5–9.5 mm. The species has a strikingly slender body compared to other female bibionines. The abdomen is long and parallel-sided, not spindle-shaped as usual for the genus.

Redescription. Male (N = 1, Fig. 37):

Total length 8.5 mm

Head: Nearly as wide as thorax when viewed dorsally. Antenna not possible to see.

Thorax: Length 2.4 mm, width 1.5 mm. Blackish brown.

Wing: Length 6.4 mm, width 2.6 mm, length/width = 2.5. Pterostigma brown, otherwise no pigmentation preserved. Humeral vein absent, Subcosta indistinctive. Vein measurements: Basal R 2.9 mm, R_1 1.4 mm, R_s 0.9 mm, R_{4+5} 2.3 mm, R-M 0.4 mm, Basal M 2.1 mm, Distal M 0.5 mm, M_1 1.8 mm, M_2 1.5 mm.

Legs: Not preserved.

Abdomen: Length 5.3 mm, width 1.7 mm. Dark brown, parallel-sided. Terminalia not preserved.

Female: (N = 1, Figs 35–36)

Total length 7.5 mm in the specimen examined, 9.5 mm in holotype according to Heer (1849: 217). Body and legs appear to have been all black, wings presumably hyaline.

Head: Length 1.0 mm. Black. Rostrum seems to be somewhat prolonged, extending about one-half the length of an antenna anterior to antennal insertion. Antennal flagellum apparently 8-segmented.

Thorax: Length 2.1 mm, 2.5 mm according to Heer (1849: 217). Entirely black.

Wing: Length 5.7 mm, 7.0 mm according to Heer (1849: 217), width 2.4 mm, 3.0 mm according to Heer (1849: 217), length/width = 2.4. Hyaline with pale brown R-veins, posterior veins colourless. Humeral vein absent, Subcosta weak and indistinctive. Pterostigma prominent and brown. Radial sector approximately twice as long as R-M. M-Cu meets M_1 some distance distal to fork. Vein measurements (N = 1 for all): Basal R 2.2 mm, R_1 1.5 mm, R_s 0.6 mm, R-M 0.3 mm, distal M 1.0 mm, M_1 2.4 mm, M_2 1.7 mm, M-Cu 0.4 mm.

Legs: Femur and most of tibia of one hind leg preserved. Black. Length of hind femur 1.7 mm (estimated), of hind tibia 2.0 mm (estimated).

Abdomen: Dark brown. Length 4.8 mm, 7.5 mm according to Heer (1849: 217), width 1.5 mm according to Heer (1849: 217).

The third specimen at the ETHZ is a female, but hardly recognisable.

Discussion. Heer (1849: 217) gave the body length as 9.5 mm, somewhat larger than the specimens we have examined. However, Heer's figure (Pl. XVI Fig. 6) suggested a specimen with a bloated, stretched abdomen, which may have increased the apparent length. The specimen examined by Heer had a similar thorax length to those we have examined. In this figure the specimen looks habitually most like a male bibionid, but since it was explicitly stated to have a small head (Heer 1849: 217) we interpret it as a female with unusually slender abdomen, like the specimens we have examined. Heer's measurements are consistently larger than the specimens we have examined, but the difference is within the degree of variability commonly seen in bibionid populations.

Genus *Dilophus* Meigen, 1803

Dilophus pumilio sp. n.

(Figs 38–40)

Bibio pumilio Heer: Cabinet name?

Material. Holotype (female) ETHZ Pl. I 886.

A single female specimen (two slabs which are apparently part and counterpart of the same specimen) in Zürich (Pl. I 886), apparently from Oeningen, labeled

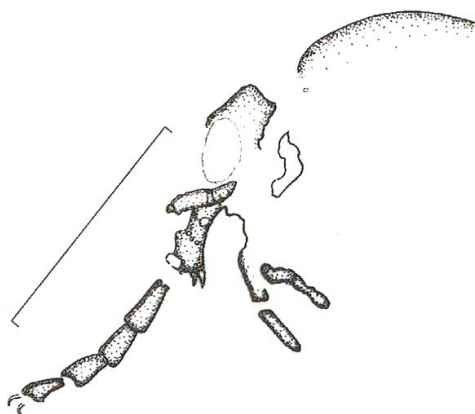


Fig. 40. *Dilophus pumilio*, ♀, forebody. ETHZ Pl. I 886.



Fig. 41. *Dilophus* sp., ♀. ETHZ Pl. I 887.



Fig. 42. *Penthetria amoena*, ♀, lectotype. SMNK Oe. 170.



Fig. 43. *Penthetria amoena*, ♀ (holotype of *Protomyia speciosa*) ETHZ Pl. I 873.

Bibio pumilio, but this name appears never to have been published. It is not well preserved, in particular the diagnostic fore tibiae and the spine rows on the anterior part of the thorax are not clearly visible. However, in the wings the crossvein R-M is markedly longer than the basal part of Rs, which is a diagnostic character for *Dilophus*.

Etymology. Name presumably given by Heer. From Latin *pumilio*, dwarf, referring to the species' small size compared to other fossil bibionids, though it is an average-sized *Dilophus*.

Diagnosis. A smallish (total length 4.5 mm) *Dilophus* with brown fumose wings. Rostrum not produced, antennal flagellum apparently with six segments. Pro-tibial spines possibly arranged 2+2 or 2+3. It differs from the other *Dilophus* known from compression fossils, *Dilophus krantzii*, most notably in being much smaller (4.5 vs. 11 mm).

Description. Habitus as in Fig. 38. Total length 4.5 mm.

Head: Length 0.8 mm. Black. Rostrum not appreciably produced. Antennal flagellum apparently six-segmented. Palp relatively long and robust, distal segment cylindrical and a little over three times as long as wide.

Thorax: Length 1.4 mm. Mesonotum black, pleurae yellowish-brown. A vague trace of pronotal spine row is preserved.

Wing: 3.8 mm long, 1.5 mm wide, length/width = 2.5. Brown fumose. Pterostigma prominent and brown, veins brownish, no difference in pigmentation between anterior and posterior veins. Measurements: Basal R 1.09 mm, R_1 0.93 mm, R_s 0.16 mm, R-M 0.34 mm, CuA_1 1.7 mm, CuA_2 1.4 mm.

Legs: Only anterior legs preserved. Brown. Probable traces of protibial spines are preserved, their exact pattern not possible to make out but may have consisted of one basal (two spines?) and one mesal (two or three spines?) group. Tarsus slender.

Abdomen: 3.0 mm long, dark brown.

Discussion. Surprisingly, this is only the second *Dilophus* species described from European compression fossils (after *Dilophus krantzii* Heyden, 1870), though there are numerous specimens known from Baltic amber (Skartveit 2009) and members of the genus are common in Europe today. The sparsity of *Dilophus* specimens in lacustrine deposits may possibly be due to behavioral differences, members of this genus not ending up in water as frequently as *Bibio* and *Plecia*. There is a second *Dilophus* female (Fig. 41) in ETHZ, labeled with the cabinet name *Bibio infernalis*. It is similar in habitus to *Dilophus pumilio* but somewhat larger, with a wing length of 4.6 mm. This specimen is obviously deformed (stretched) and reveals no important taxonomical characters, hence it is not included as a paratype.

Genus *Penthetria* Meigen, 1803

Penthetria amoena (Heer 1849) comb. n.

(Figs 42–45)

Protomyia amoena Heer, 1849

Synonym: *Protomyia speciosa* Heer, 1864. **Syn. n.**

Material. Lectotype (herein designated, Fig. 42) female: SMNK Oe. 170, Inv. 1247. This is the specimen illustrated by Heer, Taf. 17 Fig. 4. — Paralectotypes: female SMNK Oe. 159, female ETHZ Pl. I 872, female ETHZ Pl. I. 876 (labeled as *Protomyia ?macilenta*). — Additional material- female: ETHZ Pl. I 873, Fig. 43. This specimen is the one illustrated by Heer (1864: 395) and since he made no mention of other specimens should be regarded as the holotype of *Protomyia speciosa*.

Diagnosis. A medium-sized *Penthetria*, total length 9–12 mm. Antennal flagellum probably eight-segmented. Wing hyaline to slightly brownish, R_{2+3} sinuate. Legs pale brown.

Redescription. Female: Total length 9–12 mm (N = 4).

Head (Fig. 45): Brown. Length 0.9–1.4 mm (N = 3), width 1.1–1.2 mm (N = 2). Complex eye relatively large, markedly longer than occiput. Antennal flagellum probably 8-segmented. Palp with distal segment fine.

Thorax (Fig. 45): Length 2.5–3.5 mm (N = 2), width 1.7–2.1 mm (N = 2). Brown.

Wing (Fig. 44): Hyaline or slightly brownish, pterostigma indistinctive. R_{2+3} sinuate. Length 9.4–11.0 mm (N = 4), width 3.4–4.0 mm (N = 4), length/width = 2.5–3.0 (N = 4). Vein measurements: Basal R 2.4–3.2 mm (N = 4), R_1 3.6–4.5 mm (N = 4), R_s 1.9–2.4 mm (N = 4), R-M 0.5 mm (N = 4), R_{4+5} 3.9–4.9 mm (N = 4), R_{2+3} 1.2–2.0 mm (N = 4), Basal M 3.0–3.9 mm (N = 4), Distal M 0.3–1.1 mm (N = 4).

= 4), M_1 3.5–3.8 mm (N = 3), M_2 2.8–3.0 mm (N = 3), M-Cu 0.4–0.6 mm (N = 2), Basal CuA 1.9–2.4 mm (N = 2), CuA₁ 3.2–3.8 mm (N = 2), CuA₂ 2.5–2.7 mm (N = 2), A₁ 4.3–5.2 mm (N = 2).

Abdomen: Brown. Length 5.7–8.7 mm (N = 3, the former appears slightly shrunk), width 2.3–2.5 mm (N = 2).

Legs: Pale brown, slender but not particularly long. Measurements: Fore femur 2.2–2.4 mm (N = 2), fore tibia 2.3–2.7 mm (N = 2), fore first tarsomere 1.3 mm (N = 1), hind femur 2.8 mm (N = 1), hind tibia 3.3 mm (N = 1), hind first tarsomere 1.2 mm (N = 1).

Discussion. At the ETHZ there are three females (Pl. I 872) labeled as *Protomyia amoena*, but these actually belong to three different genera. One is probably conspecific with the SMNK specimens and is given paralectotype status, the second is a *Bibio* sp. (*fusiformis*?) and the third a female *Plecia* sp. with wide, elliptical wings, strikingly different from the narrow-winged *Penthetria* specimens at SMNK. Heer (1864: 395) did not provide a sufficient description of *Protomyia speciosa*, but he did refer to an illustration of the species (Heer 1864, Fig. 312), which, although in this case it is very crude, can be regarded as fulfilling the minimum criteria for considering a name validly published before 1931 (International Trust for Zoological Nomenclature 1999, 12.2.7). In addition to the specimens described above, there is a specimen in SMNK (Oe. 159) labeled as *Protomyia amoena*. This specimen is well preserved but the impression is relatively weak.

***Penthetria brevicollis* (Heer 1849).**

(Figs 46–47)

Bibiopsis brevicollis Heer, 1849, p. 231

Material. No type material seen

Discussion. The species was described by Heer (1849) as *Bibiopsis brevicollis* from Radoboj, Croatia. The type specimen was said by Heer to be in the k.k. montanist. Cabinet, but could not be located in the Naturhistorisches Museum, Vienna. One specimen at the ETHZ (Pl. I 870, Fig. 46) is identified as this species. This specimen, like the type illustrated by Heer (Pl. XV, Fig. 26) is characterized by a conspicuously small thorax and head and a wing with a strongly curved anterior edge. The antennae are comparatively large, the flagellomeres are not possible to count in the ETHZ specimen but according to the original description the type specimen has nine closely set flagellomeres. The wings in specimen ETHZ PL. I 870 (Fig. 47) appear somewhat folded and deformed, the venation appears peculiar but is difficult to interpret with certainty.

Heer (1849, 228) described the genus *Bibiopsis*, which was supposed to differ from *Penthetria* in having three branches of vein M, one of vein CuA instead of two branches of each vein as usual. The vein CuA₁ can sometimes appear to be a branch of M (as an extension of crossvein bm-cu), depending on the position and angle of M-Cu, this may have led Heer to interpreting it as a branch of M («äussere Mittelader»). The specimen from Öhningen in ETHZ is similar to *Bibiopsis brevicollis* as described by Heer (1849) in habitus and size, but until the Radoboj specimen on which Heer based his description is found and examined, this association is highly tentative. For this reason we have not attempted to redescribe the species based on the ETHZ specimen.

Genus *Plecia* Wiedemann, 1828***Plecia hilaris* Heer 1849, 211.**

(Figs 48–53)

Material. Lectotype (female, herein designated): ETHZ (specimen ... 7281, Fig. 48) looks like a mirror image of Heer's figure (Pl. XVII Fig. 6a, b) and is in all likelihood the counterpart of the specimen that Heer drew, though it is a female and not a male as stated by Heer. — Additional material, tentatively associated: male – ETHZ Pl. I 850.

Diagnosis. A medium-sized *Plecia*, wing light brown fumose. Wings distinctively pointed, cell between M and Cu narrow, apical distance between M_1 and M_2 longer than between M_2 and CuA_1 . Vein R_{2+3} short and evenly curved. Body light brownish. Male with gonostylus large and digitiform.

Redescription. Female (Figs 48, 50–51): Total length 9.5 mm (N = 1).

Head: Rather small, brown. Antenna and mouthparts destroyed, apparently during preparation of the specimen.

Thorax: Brown, length 3.1 mm (N = 1).

Wing (Fig. 50): Length 8.7 mm, width 3.2 mm, length/width = 2.7. Hyaline, veins light brown, pterostigma brown, not very prominent. Costa slightly curved. Vein R_{2+3} short and evenly curved. Vein M-Cu meets M just before or at fork. Measurements: Basal R 2.6 mm, R_1 3.4 mm, Rs 1.0 mm, R_{2+3} 0.6 mm, R_{4+5} 5.2 mm, R-M 0.3 mm, basal M 2.3 mm, distal M 1.8 mm, M_1 3.6 mm, M_2 3.1 mm, M-Cu 0.3 mm, basal CuA 1.7 mm, CuA_1 5.1 mm, CuA_2 4.2 mm, A_1 4.3 mm.

Abdomen: Yellowish-brown. Length 5.7 mm.

Legs: Brown, slender. Fore tibia length 2.7 mm (N = 1), hind tibia length 3.4 mm (N = 1).

Male (Tentatively associated, Figs 49, 52–53): Total length 10.5 mm. Habitus as in Fig. 49.

Head: Length 1.6 mm, width 1.3 mm. Antennal flagellum 7-segmented.

Thorax: Brownish-black. Length 2.6 mm, width 1.6 mm.

Wing (Fig. 52): Length 7.7 mm, width 3.0 mm, length/width = 2.6. Light brown fumose with brown veins, pterostigma brown, not very prominent. R_{2+3} relatively short and curved. Measurements: Basal R 2.9 mm, R_1 2.6 mm, Rs 1.4 mm, R_{4+5} 3.6 mm, R_{2+3} 1.0 mm, R-M 0.5 mm, basal M 3.0 mm, distal M 0.3 mm, M_1 3.0 mm, M_2 2.1 mm, M-Cu 0.6 mm, basal CuA 2.3 mm, CuA_1 3.0 mm, CuA_2 1.9 mm, A_1 4.2 mm.

Abdomen: Brown. Terminalia as in Fig. 53. Gonostylus inserted apicomesally on gonocoxite, relatively large, 0.8 mm long. Epandrium and hypandrium not preserved.

Legs: One fore leg and one tarsus, probably from mid leg, preserved. Probably dark brown. Slender, fore femur length 3.0 mm, fore tibia length 2.9 mm.

Discussion. There is one additional specimen at the ETHZ (S.N. 188) that has been identified as this species, possibly by Heer. This specimen has a long R_{2+3} and should be classified in the genus *Penthetria*.

Heer (1849, 211–212) described the genus *Protomyia*, which would differ from *Plecia* in some details in the wing venation. Heer's description of the wing venation of *Protomyia* seems to fit *Plecia* perfectly and the new genus was appar-



Fig. 44. *Penthetria amoena*, ♀, wing. ETHZ Pl. I 873.

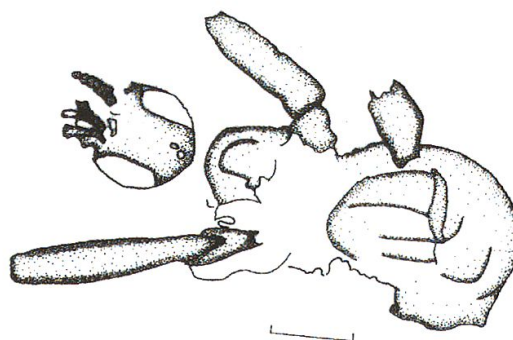


Fig. 45. *Penthetria amoena*, ♀, fore body. ETHZ Pl. I 873.



Fig. 46. *Penthetria brevicollis*, ♀. ETHZ Pl. I 870.

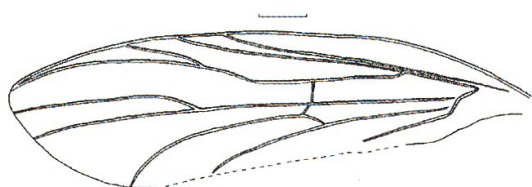


Fig. 47. *Penthetria brevicollis*, ♀, wing. ETHZ Pl. I 870.



Fig. 48. *Plecia hilaris*, ♀, lectotype. ETHZ 7281.



Fig. 49. *Plecia ?hilaris*, ♂. ETHZ Pl. I 850.

ently based on a misinterpretation of the wing venation in *Plecia*. As was already pointed out by Loew (1868), the description of the new genera *Bibiopsis* and *Proatomyia* were based on misinterpretations of the wing venations of *Penthetria* and *Plecia*, respectively.

***Plecia jucunda* (Heer 1849)**

(Figs 54–56)

Protomyia jucunda Heer, 1849, 234–235Synonym: *Protomyia affinis* Heer, 1849, 235–236. **Syn. n.**

Material. Lectotype (herein designated) female SMNK Oe. 168, Inv. 1279, Fig. 60. This is the specimen figured by Heer (1849, Taf. XVII, Fig. 2f). — Paralectotype, female ETHZ Pl. I 871, Fig. 61. This specimen is very well preserved and we believe it likely that it is one of the «sehr schön erhaltenen» specimens referred to by Heer. — Additional material (1 male 5 females): ETHZ Pl. I 853 male (part and counterpart) and female, labelled as *Protomyia macilenta* and *Plecia jucunda*, respectively, the latter by Charles Brongniart. ETHZ Pl. I 856 female — very weak impression, recognisable only to family. ETHZ Pl. I 861 female — rather weak impression labeled both as *Protomyia affinis* and *Plecia jucunda*. ETHZ Pl. I 867 female — identified by Brongniart. ETHZ Pl. I 869 female, labelled as both *Protomyia lygaeoides* and *Plecia jucunda*, the latter by Brongniart.

Diagnosis. A medium-sized *Plecia*, body black, wing elliptical, brown fumose, R_{2+3} with a bend in basal fourth, longer than in *P. hilaris*. Antennal flagellum possibly 10-segmented.

Redescription. Female: Total length 9–11.5 mm (N = 4). Habitus as in Figs 54–55.

Head: Brownish black. Length 1.1 mm (N = 1), width 1.0 mm (N = 2). Antenna relatively large, flagellum possibly 10-segmented.

Thorax: Brownish black, length 2.6–3.1 mm (N = 2), width 2.1 mm (N = 1).

Wing (Fig. 56): Length 8.8–10.0 mm (N = 4), width 3.5–4.0 mm (N = 3), length/width = 2.2–2.6 (N = 3), brown fumose, elliptical. Costa is quite curved, costal cell rather broad and a little darker than the rest of the wing. Subcosta very distinctive, running free of R in entire length. R_{2+3} with a bend in basal fourth. Crossvein R-M vertical, joins vein M approximately as far from the fork as its own length. Stem of CuA nearly as long as fork. Wing veins (N = 1 for all measures): Sc 5.2 mm, basal R 2.0 mm, R_1 3.5 mm, R_s 2.0 mm, R_{2+3} 1.1 mm, R_{4+5} 4.2 mm, R-M 0.5 mm, basal M 3.5 mm, distal M 0.6 mm, M_1 3.7 mm, M_2 2.6 mm, basal CuA 1.0 mm, CuA_1 3.4 mm, CuA_2 2.3 mm, A_1 4.3 mm.

Abdomen length 5.9–7.0 (N = 3), width 2.4–2.6 (N = 3), dark brown.

Legs: Brown, slender. Fore femur length 2.8–2.9 mm (N = 2), fore tibia length 3.0–3.3 mm (N = 2).

Discussion. The species was described from five specimens from Öhningen: two in coll. Seyfried, one in «Zürich University Museum» and two in Karlsruhe. We found eight specimens identified as this species, three of them did, however, have identification labels written by Charles Brongniart (1878). It is possible that Brongniart may have added the labels to material already identified or sorted by Heer, but this is unclear. We have chosen the specimens without Brongniart labels as lecto- and paralectotypes since these show no evidence of being identified by somebody other than Heer.

Protomyia affinis was described from one specimen from Öhningen in coll. Seyfried. We did not find the specimen depicted by Heer at the ETHZ. There is one female *Plecia* (Pl. I 861) identified as both *Protomyia affinis* and *Plecia jucunda*, apparently by Charles Brongniart. This is not the specimen described by Heer,



Fig. 50. *Plecia hilaris*, ♀, wing. ETHZ ... 7281.

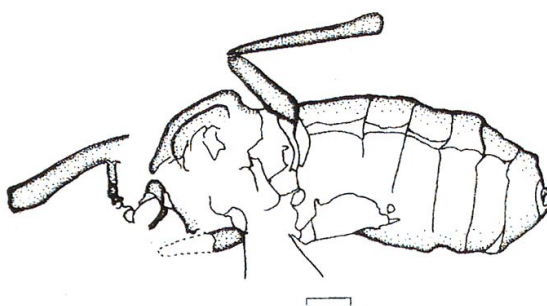


Fig. 51. *Plecia hilaris*, ♀, body. ETHZ ... 7281.

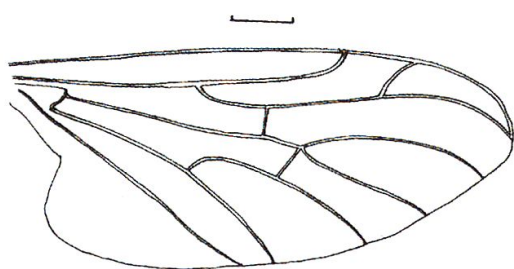


Fig. 52. *Plecia* ?*hilaris*, ♂, wing. ETHZ Pl. I 850.



Fig. 53. *Plecia* ?*hilaris*, ♂, terminalia. ETHZ Pl. I 850.



Fig. 54. *Plecia jucunda*, ♀, lectotype. SMNK Oe. 168.



Fig. 55. *Plecia jucunda*, ♀, paralectotype. ETHZ Pl. I 871.

however, and its affinity is uncertain. In the original description, Heer stated that *P. affinis* differed from *P. jucunda* mainly in being smaller. The body length given by Heer for *P. affinis* ($4 \frac{1}{8}$ lin = 8.7 mm) is only marginally outside the range of the *P. jucunda* specimens we have studied. The wing length (a much better size measure than total length) was given by Heer as $4 \frac{1}{4}$ lin. = 9.0 mm, which is within the range of the *P. jucunda* specimens we have studied. Heer (1849: 236) stated that

the wing venation of *P. affinis* was indistinguishable from that of *P. jucunda*. Thus, we believe that *Protomyia affinis* and *Protomyia jucunda* are probably synonymous.

***Plecia macilenta* sp. n.**

(Figs 57–62)

Synonym *Protomyia macilenta* Heer? (probably a cabinet name)

Synonym *Plecia pallens* Heer? (probably a cabinet name)

Material. Holotype (male) ETHZ, Pl. I 853, both part and counterpart present (Fig. 57). — Additional material: Female (ETHZ Pl. I 853). This specimen is only partly uncovered, wings obviously distorted by taphonomical processes. Female (ETHZ S.N. 186) labelled as *Plecia pallens*. Female (ETHZ Pl. I 872) labeled as *Protomyia amoena*.

Etymology. Name presumably given by Heer. Apparently from Latin *macilens*, lean or thin.

Diagnosis. A smallish *Plecia* (wing length 7–7.5 mm) with light brown fumose wings which are apically rounded. The apical distance between M_1 and M_2 is less than between M_2 and CuA_1 . Male gonostyli digitiform.

Description. Male (N = 1) Total length 11.0 mm.

Head: Length 1.3 mm, width 1.1 mm. Antenna not preserved in the specimen.

Thorax (Fig. 60): Length 2.8 mm, dark brown.

Wing (Fig. 59): Length 7.6 mm, width 2.7 mm, length/width = 2.8. Light brown fumose with brown veins, pterostigma brown, not very prominent. R_{2+3} relatively short and curved. Measurements: Basal R 2.3 mm, R_1 2.7 mm, Rs 1.3 mm, R_{4+5} 3.5 mm, R_{2+3} 0.5 mm, R-M 0.3 mm, basal M 2.5 mm, distal M 0.9 mm, M_1 2.4 mm, M_2 2.0 mm, basal CuA 2.4 mm, CuA_1 4.2 mm, CuA_2 2.3 mm, A_1 3.5 mm.

Legs: Brown. Femorae moderately clavate, tibiae slender. Not possible to measure in the specimen.

Abdomen: Length 7.4 mm, width 1.5 mm. Brown. Terminalia as in Fig. 61. Gonostylus inserted apico-mesally on gonocoxite, 0.9 mm long, digitiform. Epanandrium and hyandrium not preserved.

Female (tentatively associated, Fig. 58). Total length 11.5 mm (N = 1).

Head: Length 1.1 mm, width 1.0 mm (N = 1). Dark brown, nearly circular in dorsal view. Antenna 0.8 mm long (N = 1), flagellum 7- or 8-segmented.

Thorax: Length 3.3 mm (N = 1). Light brown.

Wing (Fig. 62): Length 7.0–9.0 mm (N = 2), width 2.8–4.2 mm (N = 2, the former measurement probably an underestimate due to folding), length/width = 2.2–2.4 (N = 2). Light brownish fumose, veins light brown, pterostigma brown, not very prominent. Costa slightly curved. Vein R_{2+3} short and evenly curved. Vein BM-Cu meets M just before or at fork. Measurements: Basal R 2.1–2.5 mm (N = 2), R_1 2.8–4.1 mm (N = 2), Rs 1.1–1.7 mm (N = 2), R_{2+3} 0.5–1.1 mm (N = 2), R_{4+5} 3.3–5.1 mm (N = 2), R-M 0.4 mm (N = 2), basal M 2.7–2.8 mm (N = 2), distal M 0.8–1.0 mm (N = 2), M_1 2.4–3.7 mm (N = 2), M_2 2.1–3.2 mm (N = 2), M-Cu 0.7–0.8 mm (N = 2), basal CuA 2.4 mm, CuA_1 3.3 mm, CuA_2 2.5 mm, A_1 3.2 mm.

Legs: Only part of femur and tibia of fore legs preserved. Light brown, slender.

Abdomen: Yellowish-brown, rather stout. Length 4.2 mm, width 1.5 mm. Terminalia not preserved.

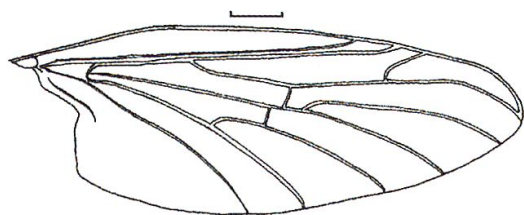


Fig. 56. *Plecia jucunda*, ♀, wing. ETHZ Pl. I 871.



Fig. 57. *Plecia macilenta*, ♂. ETHZ Pl. I 853.



Fig. 58. *Plecia ?macilenta*, ♀. ETHZ S.N. 186.

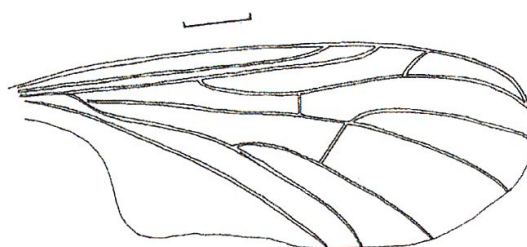


Fig. 59. *Plecia macilenta*, ♂, wing. ETHZ Pl. I 853.

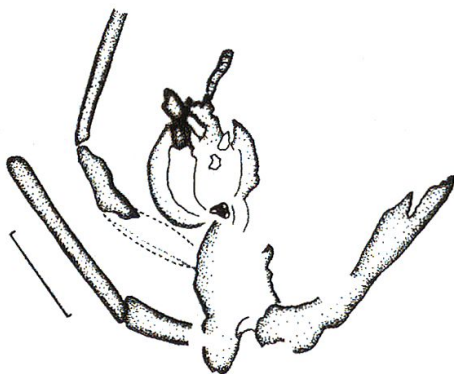


Fig. 60. *Plecia macilenta*, ♂, head and thorax. ETHZ Pl. I 853.

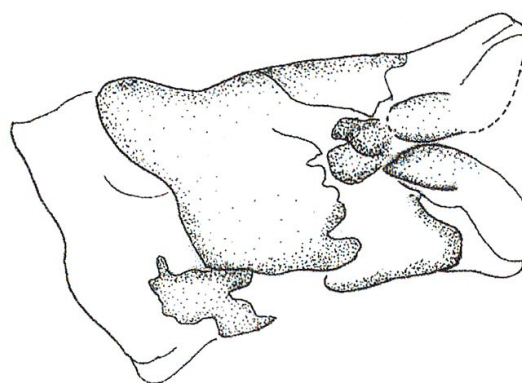


Fig. 61. *Plecia macilenta*, ♂, terminalia. ETHZ Pl. I 853.

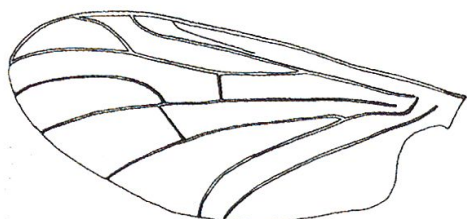


Fig. 62. *Plecia ?macilenta*, ♀, wing. ETHZ S.N. 186.

Discussion. As far as we can see, the name *Protomyia macilenta* was never published and should be regarded as a cabinet name. The association between the male and female specimens is tentative. According to an undated, handwritten list of specimens at the ETHZ the specimens labeled as *P. macilenta* and *P. pallens* may possibly originate from Aix-en-Provence, not from Öhningen. There is also another female labeled as *Protomyia ? macilenta* (ETHZ Pl. I 876). This is a female *Penthetria*, likely conspecific with *Penthetria amoena*.

KEY TO THE MORPHOSPECIES OF FOSSIL BIBIONIDS KNOWN FROM ÖHNINGEN

Females. Specimens of *Bibio obsoletus* are too poorly preserved to be included in the key.

1. Wing with vein R distally split into R_{2+3} and R_{4+5} . Profemorae slender 2
- Wing with vein R distally undivided. Profemorae conspicuously thickened (Bibioninae) 6
2. Vein R_{2+3} long and horizontal (Penthetriinae) 3
- Vein R_{2+3} short, more or less vertical (Pleciinae) 4
3. Thorax conspicuously short, wing with Costa curved . . . *Penthetria brevicollis*
- Thorax of normal length, Costa not conspicuously curved *Penthetria amoena*
4. Wing vein R_{2+3} strongly bent, basally nearly vertical *Plecia jucunda*
- Wing vein R_{2+3} nearly straight, oblique 5
5. Wing pointed, apical distance between M_1 and M_2 larger than between M_2 and CuA_1 *Plecia hilaris*
- Wing apically rounded, apical distance between M_1 and M_2 smaller than between M_2 and CuA_1 *Plecia macilenta* sp.n.
6. Smaller, body length less than 5 mm. Protibia cylindrical with spines apically and mesally *Dilophus pumilio* sp.n.
- Larger, body length at least 7 mm. Protibia more or less spindle-shaped, with a long apical spine (genus *Bibio*) 7
7. Brachypterous, wing length approximately 0.5 times body length 8
- Macropterous, wing length approximately 0.7 times body length 9
8. Larger, body length 18 mm, brownish ?*Bibio elongatus*
- Smaller, body length 13–14 mm, blackish *Bibio angustatus*
9. Wing rather narrow, hyaline with very strong, dark veins *Bibio crassinervis* sp.n.
- Wing wider, not with conspicuously strong veins 10
10. Very dark species, wing black fumose *Bibio moestus*
- Lighter coloured, wing not dark fumose 11
11. Larger, body length at least 9.5 mm 12
- Smaller, body length 7–9.5 mm 13
12. Larger, approx. 13.5 mm, body light brownish . . . *Bibio pinguis oeningensis*
- Smaller, 9.5–12 mm, body colour uncertain *Bibio fusiformis*
13. Abdomen narrow and cylindrical, parallel-sided seen from above *Bibio pulchellus*
- Abdomen stouter, more spindle-shaped, widest in the middle . . . *Bibio brevis*

GENERAL DISCUSSION

The main scope of the present paper is to redescribe and illustrate the species described by Heer (1849) from Öhningen. This is the oldest major work on European fossil bibionids, concerning an interesting fauna of sometimes reasonably well preserved specimens. Some of the taxa included were based on material which we would consider insufficient to name new species, but we have chosen to synonymise species only where we believe there is a very high likelihood that two taxa are synonymous. The only species descriptions senior to those of Heer (1849) are those of Unger (1841), whose material Heer appears to have studied. The types of the Unger species are in Landesmuseum Joanneum, Graz and have been studied by the senior author. Thus there is unlikely to be any senior synonyms for the species names here included, but several nominal species could be synonymous with each other or with subsequently described species.

In recent species of bibionoids, it is considered prudent to base any descriptions of new taxa on male specimens – this is convenient since most field-collected samples are male-biased and no case of parthenogenesis is known in the Bibionidae. The male terminalia offer valuable and presumably reliable characters for distinguishing species, particularly so in the genera *Plecia* and *Dilophus* but in other genera as well. Bibionids exhibit a very marked sexual dimorphism and associating male and female specimens in the absence of biological data (rearing, copulating specimens or field observations) can be rather difficult. In contrast, fossil materials often include a large majority of female specimens, in the material from Öhningen nearly 95 % of the specimens examined (74 out of 79) are female, and all previously described species were described based on females. Statz (1943) suggested that, given the predominance of females in the fossil record, species descriptions of fossil bibionids should be based on females only. While this may make some sense, it is problematic in that a very useful set of characters (male terminalia) are ignored, and introduces an unnecessary break between the taxonomy of fossil and recent species in a morphologically highly conservative group. A taxonomy of fossil bibionids based on females would probably have to rely heavily upon wing venation, which is of questionable systematic significance for intrageneric relationships in the Bibionidae – while each genus has its characteristic venation, it appears to be quite plastic within species with considerable variation. Also, some fossil faunas (e.g. from the French Oligocene localities at Céreste and Aix-en-Provence, Collomb *et al.* 2008) have substantial material of bibionid males.

In bibionids, there are marked differences in flight behaviour between males and females (Skartveit 2001). Samples collected in areas with high bibionid densities tend to include mostly males, while specimens trapped in areas with low density tend to be females (Skartveit, personal observation). This tendency is due to females dispersing before ovipositing, while males remain strongly aggregated. A predominance of female specimens in a sample suggests that the material does not originate from a site with high bibionid abundance, but are scattered dispersers from surrounding areas. Since bibionids are not freshwater insects, this is likely to be the case in lacustrine deposits unless they have been situated next to an area with many bibionids swarming, in which case males would be easily swept into the water by wind.

There is a notable difference between the ETHZ and the SMNK specimens in appearance. The former are mainly average to well-preserved specimens, mostly with considerable traces of organic matter, and the wing venation is generally well visible. The SMNK specimens, in contrast, are mostly quite fuzzy impressions, often with few traces of organic matter, and it is rarely possible to see all the wing veins. We can only speculate on the reasons for this difference. Possibly, Heer may have distributed the specimens between the collections, favouring his native Zurich with the best specimens and placing the less readily interpretable ones in Karlsruhe. Heer's work included material from numerous collections, most of which seem to have ended up in Zurich. One possible explanation may be that some collectors have consistently got the better specimens, by being more discerning or possibly by being willing to pay more for good specimens. Alternatively, the difference may be due to differences in storage conditions or curation during the more than 160 years since most of the specimens were collected. The Karlsruhe specimens are notable in having many rusty-coloured spots that are generally absent in the Zurich specimens and which frequently obscure important characters.

ACKNOWLEDGEMENTS

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