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The first fossil record of *Plecia* (Diptera, Bibionidae) of Greece from the Early-Middle Miocene of Kymi (Evia, Greece) and its palaeoclimatic and palaeoecological significance

ANTONIOS ISIDOROS AVRITHIS[1,*] & EFTERPI KOSKERIDOU[2]

[1]*GeoZentrum Nordbayern, Department of Geography and Geosciences, Friedrich-Alexander University Erlangen–Nürnberg (FAU), Loewenichstraße 28, Erlangen 91054, Germany*

[2]*Department of Historical Geology and Palaeontology, Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, 15774 Athens, Greece*

tonyavrithis@gmail.com; https://orcid.org/0000-0001-7813-5843

ekosker@geol.uoa.gr; https://orcid.org/0000-0001-9646-6240

**Corresponding author*

The fossil record of Bibionidae (march flies), in the Cenozoic of Europe is particularly rich compared to other families of the order Diptera (Collomb *et al*., 2008; Skartveit & Nel, 2017), and the preservation of wings in these insects makes taxonomic analyses possible in most cases. At present, *Plecia* is not recorded from Europe (Hardy, 1965), and its last occurrences are recorded in the Middle-Late Miocene (Table 1). The distribution of extant and fossil march flies has been widely used to infer temperature changes during the Cenozoic (Gentilini, 1991; Wedmann 1998, 2000; Collomb *et al*., 2008).

In this paper, we describe a new specimen of *Plecia* from the area of Kymi, Greece (tentatively assigned to the Burdigalian), the first of this genus in the country (Bachmayer *et al*., 1971, 1981; Avrithis, 2025). Furthermore, this is the southernmost occurrence of this genus in Europe and one of the last occurrences, before its hypothesized extinction at the end of Neogene due to cooling climatic conditions (Collomb *et al*., 2008). Today, species of the genus *Plecia* are widespread in the tropics while in temperate climates species of the genus *Bibio* are the dominant bibionids (Hardy, 1950, 1981, 1989).

Geological Setting. The fossil originates from Kymi municipality, Evia Island, central Greece, part of Aliveri-Kymi Basin. The exact outcrop of origin of the specimen in the area of Kymi is not known but the lithology (marl) is consistent with the characteristics of the Prinias Group of Burdigalian age rather than the younger (Tortonian-Messinian) Koustoumallou Group, which consists of conglomerates and sandstones (Riegel *et al*., 1989). The Prinias Group includes Marmarenia and Plakes formations consisting of mudstones, marls, lignites and limestones representing alternating conditions, from permanent lacustrine to swamps and ephemeral lakes (Riegel *et al*., 1989). The exact position within the formations cannot be determined for this specimen but an Early-Middle Miocene age can be concluded by the assignment to Prinias Group. Palaeobotanical interpretations suggest an Early Miocene age (Velitzelos *et al*., 2014). For the younger extent of the strata, the lower age limit is approximately 13 Ma, marked by dated volcanic rocks (Fytikas *et al*., 1976). The fine-grained lithology of the rock slab and fossil insect articulation indicate low-energy water flow conditions and the preservation of body parts indicate low oxygen conditions with some possible decay before burial. The specimen was found in old collections of Athens Museum of Palaeontology and Geology, and thus its original stratigraphic position is not known as it was not recorded in the specimen labels. However, the lithology, consisting of light brown silty marl with laminations as those found in Kymi basin and not elsewhere in Greece, are indicative of Kymi deposits, though even a relative stratigraphic position cannot be concluded as such lithology is found in multiple levels of the outcrops.

Material and methods. The specimen (MGPA-000060147) is deposited in the collections of the Museum of Geology and Paleontology, National and Kapodistrian University of Athens. The specimen was photographed with the use of a Nikon D3400 camera with AF-S Micro NIKKOR 40 mm lens mounted. The wing venation sketch was made using Adobe Illustrator CS6 software. Terminology follows Merz & Haenni (2000). All structures were measured (in mm) as preserved.

Order Diptera Linnaeus, 1758
Family Bibionidae Fleming, 1821
Genus *Plecia* Wiedemann, 1828

Plecia sp. indet.
(Fig. 1)

Material. The specimen is preserved as a compressional fossil, dorsally compressed, with left wing partly folded and abdomen, legs and head structures not well preserved.

Description. Total body length (without head) 7.8 mm, strongly compressed from dorsal side. Body entirely black. Head length and width not visible. Antennae not preserved. Thorax length *ca*. 2.6 mm and width not measurable. Legs slender partially preserved with parts of humeri and tibiae visible. Wing

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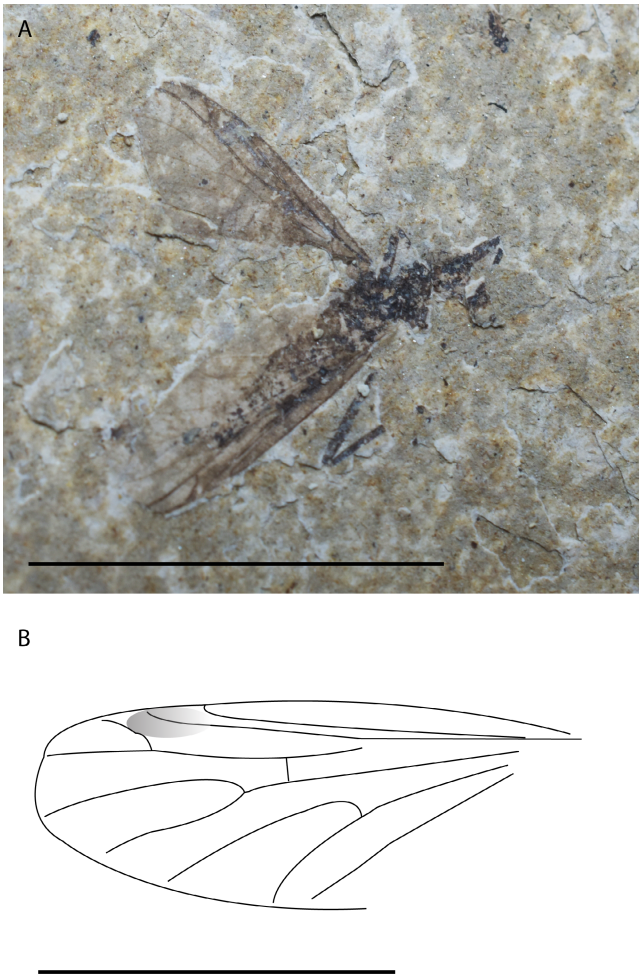

FIGURE 1. A, The fossil specimen of Plecia sp. **B**, Wing venation composite sketch. Scale bars: 10 mm (**A**); 5 mm (**B**).

length *ca*. 7.5 mm, width 2.7 mm, length/width = 2.7. Rather long and narrow wing, membrane dark brown, all veins black (strongly sclerotized originally), with costa, subcosta and radial veins being robust, black. Costal cell quite broad. Pterostigma vaguely visible. Costa well preserved. Humeral cross vein not visible. Sc long, terminates on C closer to the origin of R_{2+3} than to crossvein r-m; R_{4+5} is distally curved.

Wing veins measurements. R_{2+3}, 1.1 mm, R_{4+5}, 3.8 mm, RM, 0.4 mm, basal M, 3 mm, CuA_1 (incomplete), 2.3 mm (as preserved).

Remarks. The specimen is assigned to *Plecia* based on the characteristic wing venation pattern, particularly the configuration of veins R_{2+3} and R_{4+5}. Vein R_{2+3} basally straight and then strongly oblique, characteristic for the genus *Plecia*, while *Penthetria* has a very curved and longer vein, and this vein is completely absent in the genus *Bibio*. It has similar wing dimensions to the *Plecia* specimens found in Satovcha, Bulgaria, in terms of wing size, venational structure and size, as well as of proportions.

Discussion. *Plecia* is generally considered as an indicator of warm climates (Collomb *et al*., 2008). The occurrence of *Plecia* in the Kymi material, together with records of *Penthetria* (Bachmayer *et al*., 1971, 1981) suggests a relatively warm climate. This interpretation is consistent with palaeobotanical data indicating a warm-temperate humid environment in the region (Velitzelos *et al*., 2014). This contrasts with previous interpretations linking *Plecia* of Europe strictly to tropical climates and vegetation (*e.g*., Bulgarian records of Miocene age as noted in Simov *et al*., 2021), as paleobotanical evidence from Satovcha, Bulgaria, indicates a mixed flora with both Palaeotropical and Arctotertiary elements (Bozukov, 2002). A very similar floral composition is observed in Kymi, supporting the interpretation of a warm-temperate humid rather than fully tropical climate (Velitzelos *et al*., 2014).

The continuous cooling after the Middle Miocene Climatic Optimum led to major changes in European faunal and floral assemblages including migrations, ecological restructuring and extinctions (Kovar-Eder *et al*., 1996; Kovar-Eder, 2003; Ivanov *et al*., 2011; Eiserhardt *et al*., 2015). The Pliocene fossil record of European bibionids (*e.g*., Pliocene of Willershausen as in Skartveit *et al*., 2025) lack *Plecia* (Dürrenfeldt, 1968; Skartveit *et al*., 2025), possibly suggesting that the extinction from the European continent had already occurred at that time (Collomb *et al*., 2008), prior to the intense climatic oscillations of the Quaternary (Zachos *et al*., 2001).

Table 1 shows a gradual southward shift in the distribution of *Plecia*, from England, and North Germany in the Eocene to the Southern Balkan and Mediterranean regions by the Oligocene-Miocene. In the hothouse global conditions of the Eocene, the tropical zone was much more extended than today, and with the subsequent cooling, it was retracting (Zachos *et al*., 2001). However, palaeobotanical data suggest that even during the Early-Middle Miocene, southern Europe was characterized by mixed floras with both Arctotertiary and Palaeotropical elements, indicative of warm-temperate humid climate (Kovar-Eder, 2003).

These areas likely functioned as *refugia* for the tropical-subtropical taxa during climatic deterioration. However, in Europe the southward migration of such taxa may have been constrained by geographic barriers, particularly the Mediterranean Sea, limiting further range shifts and contributing to regional extinctions. In contrast to other continents, broader latitudinal ranges may have allowed taxa to persist in lower-latitude refugia and subsequently recolonize higher latitudes during interglacial periods.

In addition, significant tectonic changes during the Oligocene-Miocene, including the closure of the Tethys and the formation of the Mediterranean, affected humidity patterns and reduced precipitation in southern Europe (Kovar-Eder, 2003; Harzhauser *et al*., 2007). These environmental changes likely contributed to shifts in vegetation structure and ecosystem composition, further constraining the survival of *Plecia* in Europe.

These climatic and palaeogeographic factors provide a plausible explanation for the extinction of *Plecia* from Europe and may reflect broader patterns affecting other thermophilic insect taxa during the Cenozoic.

TABLE 1. List of *Plecia* occurrences in Europe (country abbreviations: FR, France; SP, Spain; BIH, Bosnia Herzegovina; BUL, Bulgaria; GER, Germany; SL, Slovenia; UK, United Kingdom).

Age	Country	Locality	*Plecia*	Citation
Pal.	FR	Menat	+	Nel & Kundura, 2024
M.Eo.	GER	Messel	+	Skartveit & Wedmann, 2015
L.Eo.	FR	Monteils	+	Collomb *et al*., 2008
E.Ol.	UK	Isle of Wight	+	Collomb *et al*., 2008
E.Ol.	FR	Barbeiras	+	Collomb *et al*., 2008
M.Ol.	FR	Chadrat	+	Collomb *et al*., 2008
M.Ol.	FR	Cereste	+	Collomb *et al*., 2008
M.Ol.	FR	Dauphin	+	Collomb *et al*., 2008
M.Ol.	FR	Les Camoins	+	Collomb *et al*., 2008
L.Ol.	GER	Enspel	+?	Wedmann *et al*., 2000
L.Ol.	FR	Aix-en-Provence	+	Collomb *et al*., 2008
L.Ol.	SL	Zasavje	+	Zalohar *et al*., 2010
E.Mio	SP	Ribesalbes, Castellón	+	Peñalver, 2002
E.Mio	SP	Rubielos de Mora	+	Peñalver, 2002
E.Mio	GER	Öhningen	+	Skartveit & Pika, 2014
M.Mio	BUL	Satovcha	+	Simov *et al*., 2021
M.Mio	BIH	Gračanica	+	Wedmann & Skartveit, 2020
L.Mio	SP	La Cerdanya	+?	Pérez de la Fuente pers. comm.
L.Mio	SP	Bellver (La Cerdanya)	+	Collomb *et al*., 2008
L.Mio	FR	Andache	+	Collomb *et al*., 2008
L.Mio	FR	St-Reine	+	Collomb *et al*., 2008

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