A new *Microphorites* in the Lower Cretaceous amber of the Southwest of France (Diptera: Dolichopodidae, “Microphorinae”)

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Abstract – A new deposit of Lower Cretaceous amber, found in Charente-Maritime (SW France) has yielded an important entomofauna with numerous arthropod associations characteristic of moist ground. We describe a new species of Dolichopodidae: ‘Microphorinae’ (Diptera: Empidoidea), *Microphorites deploegi* n. sp. on the basis of seven male and female specimens of exceptional state of preservation. This genus was previously only known from Lebanese amber of the Lower Cretaceous. The present discovery supports a reconstruction of the palaeoenvironment as a sandy beach along the sea, under a warm climate.

The “Microphorinae” is a small group of Empidoidea, with 4 recent and 3 or 5 (?) Mesozoic genera. Its taxonomic rank is still controversial. Chvála (1983) considered this lineage as a genuine family, sister-group of the Dolichopodidae. He divided it in Microphorini and Parathalassiini. Sinclair (1995) followed him on this last point but provisionally preferred to keep this group as a subfamily of the Empididae, especially because this group appears paraphyletic relatively to the Dolichopodidae, with *Parathalassius* Mik, 1891 + *Microphorella* Becker, 1909 as the sister-group of the Dolichopodidae (see the preliminary works of Colless 1963; Hennig 1971; Wiegmann *et al*. 1993). Currently, Cumming & Sinclair (2000) apparently following the conclusions of Wiegmann *et al*. (1993), included these last two genera as well as the relatively plesiomorphic genera *Microphor* Macquart, 1827 and *Schistostoma* Becker, 1902 (= *Microphorini sensu* Chvála, 1983) in the Dolichopodidae. Collins & Wiegmann (2002: 442) indicated that the “question of microphorid monophyly remains open”, even if their molecular phylogenetic study based on *Microphor* and *Schistostoma* suggests a sister group relationships between Microphorini: Microphorini and Dolichopodidae. Shamshev & Grootaert (2002: 142) proposed a new phylogenetic analysis of the “Microphorinae + Dolichopodidae lineage”, based on morphological characters, suggesting the paraphyly of the “Microphorinae”, as currently defined, with a trichotomy between *Microphor*, *Schistostoma*, and the group (Dolichopodidae + other Microphorinae).

The present discovery of numerous fossil microphorine flies in the French Albian amber is of great interest, as they belong to one of the oldest known and best-preserved fossil representatives of this group.
GEOLOGICAL SETTING
The coastal and fluvio-estuarine deposits of the Albo-Cenomanian transgression, erosive on the Kimmeridgian or Tithonian substratum, crop out widely in the Charente-Maritime region of SW France. These transgressive deposits correspond to a sand and laminated lignitic clay complex comprising two main formations (Moreau 1996): (1) at the base, which rests on an eroded Jurassic substratum, the A1 Formation, with lenticular lignitic clay containing large lumps of amber and interbedded in sands of varying thicknesses; (2) above, the younger formation A2, with laminated lignitic clay containing small lumps of amber, interbedded in fine homogeneous sands. The A1 formation is Uppermost Albian in age and the A2 formation is attributed to the Early Cenomanian (Néraudeau et al. 2002). This sequence represents a delta-filled deposit in a depressed area adjacent to the distributary channel.

The amber containing the flies described here was collected from the Albian part of the Archingeay-Les Nouillers quarry (for location, see Néraudeau et al. 2002: figs. 1, 2). This amber and the associated fossil wood were deposited in a coastal marine area, as indicated by the presence of oysters and teredinid bivalve holes in the wood and marine foraminifera in the lignitic clay.

SYSTEMATIC PALAEOENTOLOGY
Family DOLICHOPODIDAE
(sensu Wiegmann et al. 1993)
Subfamily “Microphorinae”
GENUS Microphorites Hennig, 1971
Type species: Microphorites extinctus Hennig, 1971.
Additions to diagnosis – Hennig proposed a diagnosis for this group in 1971, which was translated and summarized by Grimaldi & Cumming (1999). The present discovery confirms that the male hypopygium is rotated and lateroflexed to the right. The female tergite 10 bears no “acanthophorites’apical spines (see Sinclair 1995) and the female cercus is heavily sclerotized, held horizontally, bearing short setulae.

Microphorites deploegi n. sp.
(figs. 1-6)
Type material – Holotype specimen ARC 198.7 R (male), allotype specimen ARC 198.4 R (female).

Paratype specimens ARC 13.1 (female), ARC 78 (female), ARC 120 R (male), ARC 196 R (male), ARC 200.1 R (female), ARC 118 R (female). Other specimens: ARC 116.3 R (female), ARC 117 (male). All in Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France.

Type locality: Archingeay-les-Nouillers, Charente-Maritime, France.
Etymology – After M. Gaël De Ploëg, for his kind and efficient help in collecting and preparing the fossil insects in amber.

Figure 1
Microphorites deploegi n. sp., holotype specimen ARC 198.7 R, Photograph.

Figure 2
Microphorites deploegi n. sp., holotype specimen ARC 198.7 R, Photograph of the head and thorax.
Stratigraphic horizon – Lower Cretaceous, Uppermost Albian (Néraudeau et al. 2002).

Description – Male. Whole body 0.90 mm long. Head 0.26 mm high, 0.18 mm long; eyes bare, very large, not emarginated near antennae, holoptic, all ommatidia of equal size; small ocellar triangle somewhat prominent posterior to eyes; proboscis visible with relatively long labium; palpus one-segmented, short but longer than broad, 0.04 mm long, not appressed to labrum, and bearing one strong and two weaker setae; antenna placed below middle of head; pedicel 0.02 mm long, with crown of long setae, distinctly shorter than first flagellomere, 0.14 mm long; second + third flagellomeres 0.24 mm long, terminally situated on and only slightly longer than first flagellomere; second flagellomere short; third elongate, bearing only one terminal bristle; antennal style-type stylate (sensu Wiegmann et al. 1993).

Thorax 0.36 mm long; scutum moderately arched; proepisternum and prosternum bare; relation (separation or fusion) between these two sclerites not discernable; some strong thoracic setae; scutellum high with 2 long apical setae; laterotergite bare; prothoracic precoxal bridge not discernable.

Legs bristly. Hind femur with dorsal row of 14 setae of about equal length, longest setae 2/3 width of femur; hind tibia not clavate, equal in width to fore and mid tibia; first hind tarsomere of normal shape, not expanded and flattened, with apical comb of 3-4 short setae; empodium setiform; pulvilli well-developed; hind coxa 0.12 mm long; hind trochanter 0.14 mm long; hind femur 0.38 mm long, 0.08 mm wide; hind tibia 0.40 mm long; hind basitarsus 0.14 mm long, 0.02 mm wide; distal part of hind tarsus 0.22 mm long; mid coxa 0.12 mm long; mid trochanter 0.12 mm long; mid femur 0.32 mm long, 0.02 mm wide; mid tibia 0.34 mm long; mid basitarsus 0.22 mm long, 0.02 mm wide; distal part of mid tarsus 0.26 mm long; fore coxa 0.04 mm long; fore trochanter 0.04 mm long; fore femur 0.32 mm long, 0.02 mm wide; fore tibia 0.34 mm long; fore basitarsus 0.14 mm long, 0.02 mm wide; distal part of fore tarsus 0.24 mm long.

Wing not pointed at apex, 0.90 mm long, 0.40 mm wide; venation radiating: main veins not parallel; branches of R not particularly thickened; veins not setose, except C; C with one row of strong spinules; C ending between R4 + 5 and M1; Sc curved posteriorly towards R1, closely parallel with R1 but not touching it, and less distinct in its distal part; Rs originat-
in *Microphorites deploegi*. He also characterized this group by several venational characters: (A) base of Rs arising opposite cross-vein h; (B) Rs 2-branched, R4 + 5 unforked; (C) basal cell and anal cell shortened; (D) vein closing anal cell curved; vein A1 very short; (E) alula not developed. All these characters are present in *Microphorites deploegi*. Character (A) is also present in Dolichopodidae. Chvála (1983) added the potential character “anal lobe not developed”, present in *Microphorites deploegi*, Dolichopodidae, Microphoridae except *Microphor* and *Schistostoma*. Chvála (1983) regarded the well-developed anal lobe of these last two genera as a secondarily apomorphic condition.

According to Wiegmann et al. (1993), the clade [“Microphorinae” (= *Microphor* + *Schistostoma*) + (“Dolichopodidae” + “Parathalassinæ” (= *Parathalassius* + *Microphorella*))] is supported by the following potential synapomorphies: M with two branches; male abdominal sternite 8 pleural; presence of microphorid hypopygial asymmetry; hypopygium rotated. All these characters are present in *Microphorites deploegi*, except for the ventroflexion of the hypopygium. If this structure is rotated in “Microphoridae”, it is not in a ventral but a lateral position.

In Wiegmann et al. (1993)’s cladistic analysis, the “Microphorinae” and “Parathalassinæ” were represented by *Microphor sycopeantor* and *Parathalassius* respectively. They gave the following character states to support the clade “Microphorinae”, all homoplastic within the Empidoidea: (1) Antennal style stylate: according to their study, the polarity of this character state is somewhat uncertain. It is present in *M. deploegi*, whereas the antennal style is aristate in the parathalas-

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any value to this character, indicating that it has a specific origin in the various subfamilies of dolichopodids. (9) eyes pubescent: this character is not shared by *M. deploegi*. This character is currently considered a strict synapomorphy of (“Dolichopodidae” + “Parathalassiinae”) (see also Hennig 1971; Chvála 1983), but Negrobov (1987) denied its value, without further argument. (10) Antenna inserted high on face: *M. deploegi* and *Microphor* do not share this character. (11) Propisternum bare: this character is shared by *M. deploegi*. (12) Sc (Subcosta) termination very reduced: even if Sc is reduced in *M. deploegi*, it is less than in the (“Dolichopodidae” + “Parathalassiinae”). (13) Anal lobe reduced: if the anal lobe of *M. deploegi* is more reduced than in *Microphor*, it is broader than in *Microphorrella* (see Chvála 1983: figs. 604-605). It is difficult to estimate the state of this continuous character in *M. deploegi*.

This species does not share the autapomorphic character states of the “Dolichopodidae” (Sc ending in R1, structure of male genitalia, only one medial branch). The unique potential autapomorphy (homoplastic) for the “Parathalassiinae” proposed by Wiegmann *et al.* (1993), concerns tergite 10 but it is not visible in *M. deploegi*.

In conclusion, according to Wiegmann *et al.* (1993), *M. deploegi* falls into the clade [“Microphorinae” + (“Dolichopodidae” + “Parathalassiinae”)]. It would share no potential synapomorphy with the (“Dolichopodidae” + “Parathalassiinae”). It would share one potential synapomorphy (character state 1 above) with the “Microphorinae”, but of uncertain value and polarity.

Sinclair (1995) considered that the phylogenetic hypotheses proposed by Wiegmann *et al.* (1993) are poorly supported. Sinclair (1995) added the structure of the female cercus, which are heavily sclerotized, as in *M. deploegi*, as a synapomorphy of the [(Trichopezinae + Brachystomatinae + Ceratomerinae) + (“Microphorinae” (= Microphoridae sensu Chvála 1983) + “Dolichopodidae”)]. The partial fusion of sternite and tergite 8, possibly present in *M. deploegi*, could also correspond to the second synapomorphy of this clade (Sinclair 1995).

After the phylogenetic analysis of Shamshev & Grootaert (2002), *Microphorites deploegi* shares with the clade (modern “Parathalassiini” + Dolichopodidae) the following synapomorphy “costal vein with one row of spines”, but not the other synapomorphy “stylus one-segmented”. The three other synapomorphies of this clade are unknown in *M. deploegi*, viz. precoxal bridge complete, male tergite 8 absent, female tergite 8 divided. Thus, it could fall as sister group of this clade.

On the contrary, after the phylogenetic analysis of Cumming & Brooks (2002) based on a different set of characters, the genus *Microphorites* would fall in the same clade with the two modern genera *Schistostoma* and *Microphor*, supported by the reduction of the female acanthophorous spines and anal vein A1 absent. Both characters are subject to homoplasy in their analysis, unlike the character concerning the vestiture of costal vein, after Shamshev & Grootaert (2002). Nevertheless, *Microphorites* has not one of the two synapomorphies supporting the other clade (Parathalassini & Avenaphora & Dolichopodidae) proposed by Cumming & Brooks (2002), i.e. “male eye separation dichoptic”, but it has the other one “costa incomplete”.

In conclusion, *M. deploegi* is related to the group (“Microphorini” + “Dolichopodidae” + “Parathalassiini”), and more probably to the “Dolichopodidae” + “Parathalassini” than to the “Microphorini”, contra Hennig (1971: fig. 1). But its phylogenetic relationships would need further investigation.

It also differs from the modern and Cenozoic representatives of the genera *Microphor* and *Schistostoma* in its small anal lobe. *Microphorites deploegi* shares with *Microphor* the abdominal sternites with bristles, even if they are stronger in *M. deploegi*. These bristles are absent in *Schistostoma* (Chvála 1987).

**Comparison of Microphorites deploegi with the fossil taxa attributed to the Microphoridae**

*Microphorites deploegi* strongly differs from *Microphor rusticus* (Meunier, 1908) (Upper Eocene, Baltic amber) in its anal vein not extending in the anal lobe (Meunier 1908; Hennig 1971). *Microphor eocenica* (Meunier, 1902) (Upper Eocene, Baltic amber, male specimen, originally attributed to the genus *Holoclera*, transferred into *Microphor* by Melander (1927: 372), in the empidid genus *Rhamphomyia* Meigen, 1822 by Hennig (1971), but listed again in *Microphor* by Evenhuis 1994: 351). It differs from *Microphorites deploegi* in its wide anal lobe, with a long vein A1. *Microphor defunctus* (Handlirsch, 1910) (originally named “Microphorus defunctus”, Upper Eocene?, Tulameen River, British Columbia, Canada) is known after an apparently rather poorly preserved specimen. Its wing venation is similar to that of a Microphoridae, but vein Sc is poorly figured by Handlirsch (1910: fig. 33) and nothing is known about the veins CuA2 and A1. Its attribution to *Microphor* (in fact to the Microphorini sensu Chvála 1983) is only supported by the posterior tibia and basitarsus “somewhat terminally expanded”. There is no character available for a correct comparison with other recent and fossil...
taxa. This species can only be considered a possible Microphorini of uncertain affinities.

_Electrophorella_ Cumming & Brooks, 2002 (two species _E. baltica_ Cumming & Brooks, 2002 and _E. grimaldii_ Cumming & Brooks, 2002, both from Upper Eocene Baltic amber) differs from _Microphorites deploegi_ in the absence of the base of anterior portion of cross-vein m-cu such that M2 appears to curve continuously as a branch off of CuA1, and in the possession of a single-segmented stylus (Cumming & Brooks 2002).

_Cretomicrophorus rohdendorfi_ Negrobov, 1978 (Santonian, Upper Cretaceous, Taymyr amber, Siberia) and _C. novemundus_ Grimaldi & Cumming, 1999 (Turonian, Upper Cretaceous, New Jersey, USA) have their cells bm and dm not separated because vein bm-cu is incomplete. Chvála (1983) discussed the first species and considered that it could belong to the dolichopodid lineage because of the fusion between cells bm and dm. This hypothesis is potentially supported by the analysis of Shamshev & Grootaert (2002) who considered this character as a synapomorphy of the clade (Dolichopodidae + (Parathalassini + Microphorella)). Grimaldi & Cumming (1999: 63) put this genus in the Parathalassini.


The male of _Avenaphora hispida_ Grimaldi & Cumming, 1999 (Lower Cretaceous, Lebanese amber) has clearly dichoptic eyes, unlike _M. deploegi_.

_Microphorites extinctus_ Hennig, 1971 (Neocomian, Lower Cretaceous, Lebanese amber) is only based on a female specimen. It is not possible to compare the male structures with those of _M. deploegi_. It has four strong setae on the scutellum, instead of two in _M. deploegi_. Nevertheless, they have very similar body structures, the same wing venation, especially in the median, cubital and anal veins. Also they share the same structure of Sc, distinctly curved posteriorly towards R1, closely parallel with it but not touching it, and less distinct in its distal part. _Microphorites similis_ Grimaldi & Cumming, 1999 (Neocomian, Lower Cretaceous, Lebanese amber, based on a female specimen) has also two pair of setae on the scutellum. After Grimaldi & Cumming (1999: fig. 37), its Sc is not curved posteriorly towards R1. It also differs from _M. deploegi_ in its vein C ending at R4 + 5, instead of between R4 + 5 and M1. _Microphorites oculeus_ Grimaldi and Cumming, 1999 (Neocomian, Lower Cretaceous, Lebanese amber, male specimen) also differs from _M. deploegi_ in the same character. _Microphorites deploegi_ and _M. oculeus_ greatly differ in the ornamentation of their hypopygium: the anterior expansion is smaller in _M. oculeus_ than in _M. deploegi_ and the posterior expansion is more posteriorly directed in _M. oculeus_ than in _M. deploegi_ (compare Figures 4-6 to Grimaldi & Cumming 1999: fig. 38). The male of _M. deploegi_ has strong bristles on the ventral part of abdominal sternites, unlike _M. oculeus_ (not cited in Grimaldi & Cumming 1999). The absence of ‘acanthophorites’ spines in female _M. deploegi_ confirms the assumption of their absence in the other species of _Microphorites_ (Grimaldi & Cumming 1999: 57).

Note. The main difference between _M. similis_ and _M. oculeus_ is the “longer and more abruptly tapered” flagellum. Such a character is difficult to appreciate because the aspect of the flagellum in these species depends on the angle of view. Further discoveries of male specimens shall be necessary to confirm the specific differences between these Lebanese fossil flies.

Modern European species of microphorid flies inhabit sandy biotopes. _Microphor_ spp. prefer “lowlands close to water or deciduous forests” (Chvála 1983). As the exact relationships between _Microphorites_ and the modern “Microphorinae” remain obscure, it is not possible to infer any accurate biological information based on its phylogenetic affinities (Nel 1997). Nevertheless, the specialized female genitalia shared by recent “Microphorinae” and _Microphorites_ could correspond to a “functional adaptation of significance for oviposition”, related to sandy biotopes (Chvála 1983: 72). Interestingly, Lourenço (submitted) described a fossil scorpion that “may represent an element living on litter rather than an arboricolous element” in the same amber. A Gryllotalpidae described from the amber of Archingeay, which is functionally adapted to sandy environments (Perrichot et al. 2002), supports the hypothesis that the resin was produced by plants growing in or close to such an environment, maybe a sandy beach along the sea.
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