

First evidence of *Mastigophora* (Cephalopoda: Coleoidea) from the early Callovian of La Voulte-sur-Rhône (France)

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A 3-dimensionally preserved coleoid cephalopod from the Lower Callovian La Voulte-sur-Rhône *lagerstätte* is described. The comparison with *Mastigophora brevipinnis* from the Upper Callovian Oxford Clay of Christian Malford (U.K.) revealed remarkable similarities in their soft part morphologies. The shared presence of conspicuously short arms, one pair of near-terminal and ear-shaped fins, and an unusual thickening of the anterior mantle margin led the author to determine the specimen under investigation as *Mastigophora* aff. *brevipinnis*. The presence of uniserial and ringless suckers in *Mastigophora* aff. *brevipinnis* support a phylogenetic relationship with the Vampyropoda rather than with the Decabrachia. The previously discussed presence or non-presence of tentacles in *Mastigophora* is re-evaluated.

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Introduction

Besides the Nusplingen (Upper Kimmeridgian), Solnhofen (Lower Tithonian) and Hakel (Cenomanian) Plattenkalks, other fossil *lagerstätten* such as the Oxford Clay of Christian Malford (Upper Callovian) and the La Voulte-sur-Rhône *lagerstätte* (Lower Callovian) belong to the most important evolutionary windows through which observation of ancient life is possible. Such *lagerstätten* are outstanding not only due to their high diversity, but also due to their extraordinary preservation of fossilised soft tissues. Particularly, teuthologists benefit from these enormous information sources (e.g., Fischer & Riou 1982; Donovan 1983; Fischer & Riou 2002; Klug et al. 2005; Fuchs 2006a; Fuchs et al. 2009; Klug et al. 2010; Fuchs & Larson 2011a, 2011b). Remarkably, the Christian Malford *lagerstätte* even became famous through its excellent soft

part preservation of *Mastigophora*, a gladius-bearing coleoid previously known only from the Oxford Clay (Owen 1856; Donovan 1983; Wilby et al. 2008). Based on its unique gladius morphology, Engeser & Reitner (1985) established the family Mastigophoridae. The Mastigophoridae are today grouped together with the Loligosepiidae and Leptotheuthididae in the Loligosepiina. Owing to conspicuous gladius similarities, the Loligosepiina is often regarded as a stem-group of the Vampyromorpha with its only living representative *Vampyroteuthis infernalis*, the vampire squid (Engeser 1988; Page & Doyle 1994; Doyle et al. 1994; Fuchs 2006a, 2006b; Fuchs & Weis 2008).

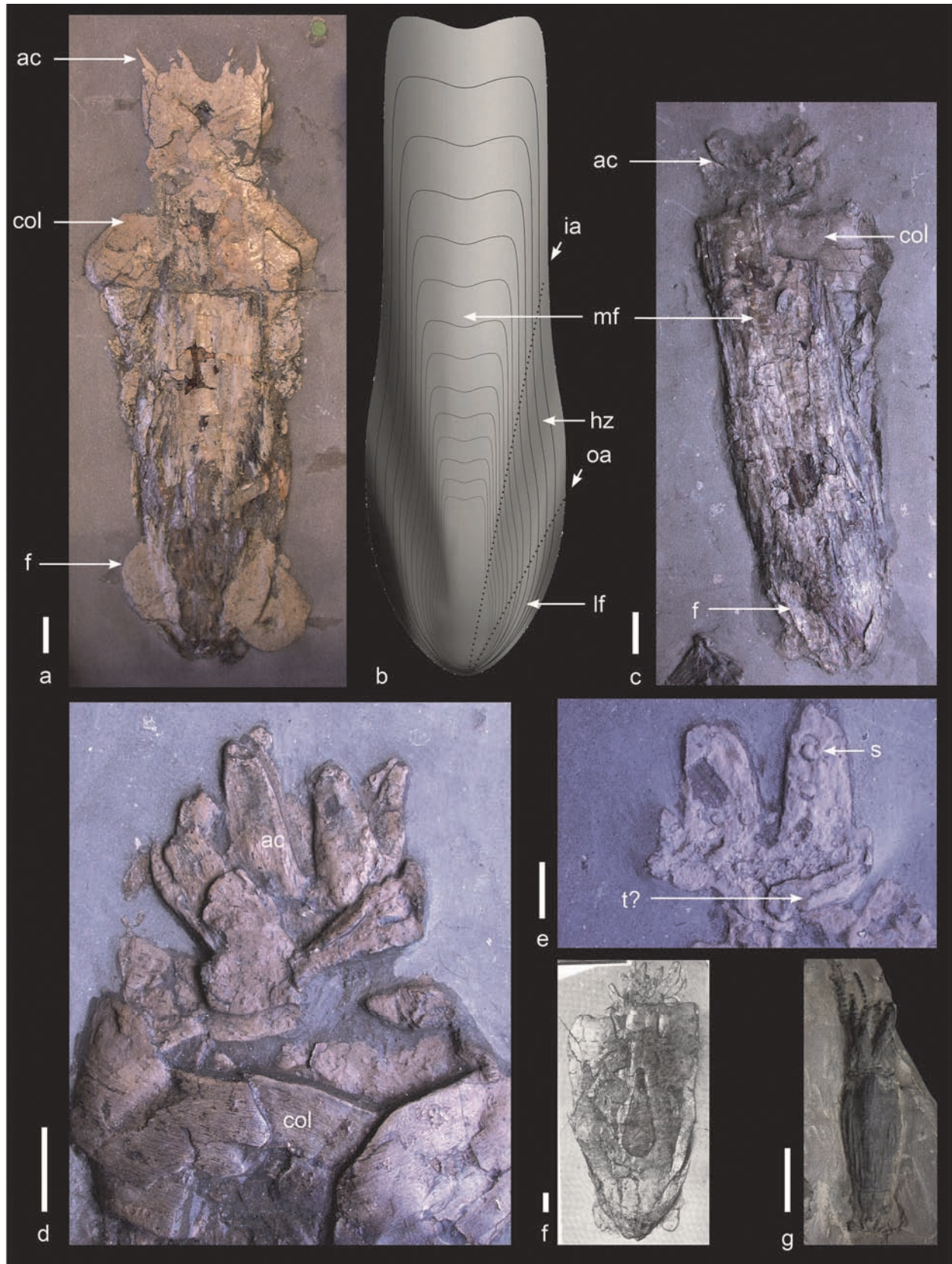


Fig. 1: (a–f) *Mastigophora brevipinnis* Owen, 1856, Christian Malford (U.K.), Upper Callovian, *athleta* Zone. (a) BMNH C.25288 [original of Donovan 1983: fig. 2], dorsal view; (b) gladius reconstruction, dorsal view; (c) BMNH C.88606, dorsal view; (d) BMNH C.25287 [original of Donovan 1983: fig. 7b], ventral view; (e) BMNH C.32352 [original of Vecchione et al. 1999: fig. 5]; (f) BMNH C.2695 [neotype, original of Donovan 1983: fig. 1], ventral view. (g) *Mastigophora* aff. *brevipinnis*, La Voulte-sur-Rhône (France), Lower Callovian, *koenigi* Zone, MNHN 74241 [original of Fuchs 2006a: pl. 21, fig. D], dorsal view. All scale bars: 10 mm. Abbreviations: ac = arm crown, col = collar, f = fins, hz = hyperbolar zone, ia = inner asymptote, lf = lateral field, mf = median field, oa = outer asymptote, s = sucker, t = tentacle.

This systematic assignment implicates that *Mastigophora* belongs to the “pseudo-eight-armed” (8 plus 2 rudimentary arms) lineage on the vampyropod branch. This attribution is challenged by findings made by Owen (1856) and more recently by Vecchione et al. (1999), who presumed that tentacles were present in *Mastigophora*. The presence of a strongly modified arm pair in ventrolateral position would strongly suggest decabrachian affinities rather than octobrachian. In the light of this controversy, *Mastigophora* is – similar to other taxa such as *Plesiotheuthis* (see discussions in Fuchs et al. 2007b) and *Palaeololigo* (see Donovan & Strugnell 2010) – a key taxon in the principle discussion on whether Mesozoic gladius-bearing coleoids represent fossil vampyropods or teuthids.

In the paleontological collection of the Musée National d’Histoire Naturelle Paris (MNHN), an undetermined specimen from the La Voulte *lagerstätte* attracted my interests because it shows soft-tissue features typical for slightly younger *Mastigophora brevipinnis* from the Oxford Clay (Figs. 1a–f). It is hence the aim of the present article to describe and discuss this 3-dimensionally preserved specimen with a special focus on the arms and thus the systematic assignment of the genus.

Material

The specimen (MNHN 74241) comes from La Voulte-sur-Rhône (Ardèche, France), a locality of Early Callovian age (*koenigi* Zone; Fig. 2) and famous for its 3-dimensional soft part preservation. According to Wilby et al. (1996: 848), “The soft tissues in the specimens are replaced mainly by apatite and pyrite, intervening areas are filled with calcite.” The specimen co-occurred with other gladius-bearing coleoids such as *Romaniteuthis gevreyi*, *Rhomboteuthis lehmani*, *Vampyronassa rhodanica*, and *Tendopsis* sp. (Fischer & Riou 1982, 2002; Fischer 2003). These taxa were likewise studied during my stay at the MNHN.

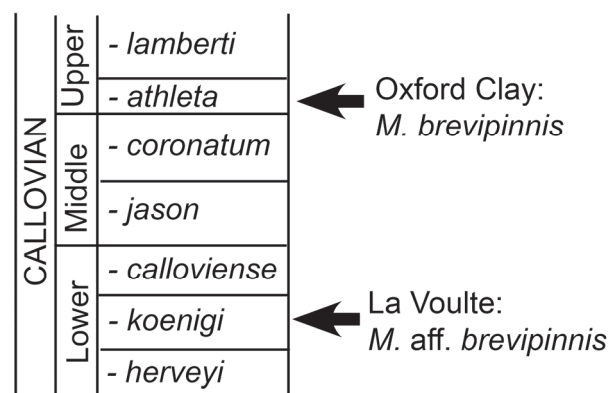


Fig. 2: Stratigraphic occurrences of *Mastigophora brevipinnis* and *Mastigophora aff. brevipinnis*.

Sixteen specimens of *Mastigophora brevipinnis* from the Upper Callovian Oxford Clay of Christian Malford (*athleta* Zone) were subject to morphological comparisons. The latter specimens are housed in the palaeontological collection of the British Museum of Natural History (BMNH).

Systematic palaeontology

Superorder **Vampyropoda** von Boletzky, 1992

Order **Vampyromorpha** Robson, 1929

Suborder **Loligosepiina** Jeletzky, 1965

Included families. – Loligosepiidae Van Regteren Altena, 1949; Leptotheuthididae Naef, 1921; Mastigophoridae Engeser & Reitner, 1985.

Family **Mastigophoridae** Engeser & Reitner, 1985

Diagnosis (after Fuchs 2006b). – Mastigophoridae includes forms with short lateral fields and particularly broad and elongated (outstretched) hyperbolar zones. “Hyperbolar” growth lines are almost straight, i.e. only weakly curved inwards. Hyperbolar zones are therefore not developed as furrows. As a result, transition from the short lateral fields into the longer hyperbolar zone is smooth. Inner and outer asymptotes are therefore indistinct.

Type genus. – *Mastigophora* Owen, 1856.

Included genera. – *Mastigophora* Owen, 1856; *Doryanthes* Münster, 1846; *Bavaripeltis* Engeser & Keupp, 1997.

Geographical and stratigraphical occurrence. – Middle Jurassic (Callovian) – Late Jurassic (Tithonian) of Europe.

Remarks. – Originally, the Mastigophoridae included only the genus *Mastigophora* (Engeser & Reitner 1985: 248; Engeser 1988: 25). Engeser & Keupp (1997) later added the genera *Bavaripeltis* Engeser & Keupp, 1997 and *Donovaniteuthis* Engeser & Keupp, 1997. Fuchs (2006b: 87), in his revision of the family, mentioned doubts about the classification of *Donovaniteuthis*. He removed *Donovaniteuthis* and instead included the genus *Doryanthes* Münster, 1846. Additionally, Fuchs (2006b: 82) preliminarily included the genus *Boreopeltis* Engeser & Reitner, 1985. Fuchs et al. (2007b) and Fuchs & Larson (2011a), however, followed Engeser (1988) and placed *Boreopeltis* in the proto-teuthid Plesiotheuthididae. Fuchs (2006b: 87) also mentioned the possibility of a mastigophorid record from the Aptian of Central Russia (see Hecker & Hecker 1955: fig. 1), but re-investigation of this specimen has shown more similarities with a plesiotheuthid gladius (unpublished data).



Fig. 3: (a–f) *Mastigophora* aff. *brevipinnis*, La Voulte-sur- Rhône (France), Lower Callovian, *koenigi* Zone), MNHN 74241 [original of Fuchs 2006a: pl. 21, fig. D]. (a) specimen in dorsal view; (b) head and arm region in dorsal view; (c) dorso-lateral view of the funnel; (d) posterior mantle in dorsal view; (e) arm crown in anterior view; (f) arm crown in lateral view. Scale bars: (a) = 10 mm, (b–d) = 1 mm.

Genus *Mastigophora* Owen, 1856

Type species. – *Mastigophora brevipinnis* Owen, 1856.

Included species. – Only *Mastigophora brevipinnis* Owen, 1856.

Geographical and stratigraphical occurrence. – Oxford Clay of Christian Malford, Wiltshire, U.K. (Upper Callovian, *athleta* Zone) and La Voulte-sur-Rhône (Lower Callovian, *koenigi* Zone).

Mastigophora aff. *brevipinnis* Owen, 1856

Fig. 3

Material. – 1 specimen (MNHN 74241; original of Fuchs 2006a: pl. 21, fig. D).

Origin. – La Voulte-sur-Rhône (Lower Callovian, *koenigi* zone).

Description. – Specimen MNHN 74241 shows a 3-dimensionally preserved soft body including mantle, head and arm crown (Fig. 3a). The posteriorly rounded mantle has a maximum length of 29 mm and a maximum width of 7 mm. Vague imprints on both sides of the posterior mantle suggest a pair of near-terminal and ear-shaped fins (Fig. 3d). A gladius is not visible; it is most probably covered by mantle musculature. Close to the collar-like thickened anterior mantle margin, a median elevation withdrawn from the muscular mantle is interpreted as the funnel (Figs. 3b–c). The fossil is hence exposed in ventral view. This interpretation is supported by the position of the eyes, which are perceptible on both dorso-lateral sides of the head (Fig. 3f). The head is separated from the collar-like thickened anterior mantle margin by a distinct furrow (Fig. 3b). The arm crown preserves 5–6 short arms (length 8 mm; ratio arm length / mantle length = 0.26) with noticeably thick arm bases (Figs. 3b, e–f). Two further arms are distinctly longer (12 mm). According to the ventral view, this elongated arm pair is unambiguously in dorsal position. Oral surfaces of both dorsal arms indicate the presence of uniserial circular suckers (Figs. 3b, e–f). The latter arm pair clearly lacks tentacular clubs. There is no evidence of cirri or hooks (onychites).

Comparison with *Mastigophora brevipinnis* from the Upper Callovian Oxford Clay of Christian Malford

A mantle length of less than 30 mm is noticeably shorter than in *M. brevipinnis* from the Oxford Clay (compare mantle lengths in Figs. 1f, g). Mantle lengths in *M. brevipinnis* range from 120 to 300 mm. Hence, one might regard *Mastigophora* aff. *brevipinnis* as a juvenile (see discussion below). Admittedly, Recent squids are known to exhibit significant morphological differences during their ontogeny so that a meaningful comparison is certainly problematic. On the other side, a congeneric (if not con-

specific) affinity appears comprehensible since morphological similarities are striking.

Similar to *M. aff. brevipinnis*, the body of *M. brevipinnis* is mainly characterised by obviously short arms and a pair of near-terminal and ear-shaped fins. Moreover, both taxa under discussion share an unusual thickening of the anterior mantle margin. Although the gladius cannot be studied, it is obvious that the gladius shape of *M. brevipinnis* matches well within the tubular mantle outline of the La Voulte specimen (Fig. 1b).

A distinctly elongated arm pair has also been described in the British *M. brevipinnis* by Vecchione et al. (1999: 115). However, those arms appear considerably longer than in the French specimen. Besides, these strongly extended structures lack suckers, in contrast to the dorsal elongated arm pair of the La Voulte specimen.

Comparison with other loligosepiids

A comparison with closest relatives of *Mastigophora*, *Doryanthes* and *Bavaripeltis*, is unfortunately impossible as soft parts are still unknown in the latter genera.

Among other loligosepiids, comparatively short arms and a pair of near-terminal and ear-shaped fins are known in *Leptotheuthis gigas*, a gigantic loligosepiid from the Upper Jurassic of Solnhofen (South Germany). Lower Jurassic *Loligosepia aalensis*, on the other hand, has been recently described to have evidently longer arms (Fuchs et al. 2013). Although mantle musculature is commonly preserved in Lower Jurassic loligosepiids such as *Jeletzkyteuthis*, *Geopeltis* and *Parabelopeltis*, nothing is known about their arm- or fin- morphology (Fuchs & Weis 2008).

Discussion

The taxonomy of Mesozoic gladius-bearing coleoids is exclusively based on gladius morphologies. However, it is worthwhile to note that with increasing knowledge about soft part morphologies, we are more and more realising that soft parts are often highly congruent within subgroups. The possession of two pairs of fins, for instance, is unique for *Trachyteuthis* as well as for its closest relative *Glyphiteuthis* (Donovan 2002; Fuchs et al. 2007a; Fuchs & Larson 2011b). Both genera additionally exhibit a moderate arm length. On the other hand, closely related taxa with a similar gladius morphology and a strikingly dissimilar soft-part morphology are unknown. In the light of this, it is conceivable to consider the shared presence of very short arms, one pair of near-terminal and ear-shaped fins, and an unusual thickening of the anterior mantle margin at least as congeneric characters.

Accordingly, two alternative interpretations are possible: 1) early Callovian *Mastigophora* from La Voulte is either a juvenile very similar to its adult stage or 2) the latter is an adult (or subadult) significantly smaller than their late

Callovian descendants. Both ideas extend the stratigraphic and biogeographic distribution of the genus *Mastigophora*. What can Lower Callovian *Mastigophora* from La Voulte contribute to the principle discussion on the total number of arms in Mesozoic gladius-bearing coleoids? Fact is that despite the outstanding state of preservation there is no evidence of ventro-lateral tentacles, which typify decabrachian coleoids; and also in Upper Callovian *Mastigophora*, the presence of tentacles is questionable. Donovan (1983), who counted only eight arms in the neotype of *Mastigophora brevipinnis*, could not confirm true tentacles described by Owen (1856). Interestingly, Donovan (1983: 491) stated: “One or two examples, such as 25288 (...) which appear to show the filaments, probably do so either, because the outline of the arms has been carved in order to produce a more acceptable fossil. This problem exists with a number of specimens in which it is not possible to be quite certain that the outline of the head and arms has not been affected by attempts to prepare the fossil when the shale was fresh and soft.”

Hence, coleoids from Christian Malford have unfortunately been “improved” through idealised carving, leaving slightly falsified soft tissue outlines (see also Wilby et al. 2008: 95). This becomes a particular problem in questions concerning the total number of arms.

Later, Vecchione et al. (1999) based on new material recognised structures that appear to represent the stalks of tentacles. However, similar to Haas (2002: 344), I have some doubts about their interpretation (see Fuchs 2006a: 74), because the presumed existence rests upon slightly thinner arm bases (see Fig. 1e). Indeed, these presumed tentacular stalks appear to lack suckers. On the other side, this is the case in most arms of *Mastigophora* from the Oxford Clay, where suckers are preserved only sporadically (compare Figs. 1d–e).

In the distal region of regular arms, Vecchione et al. (1999) additionally observed strongly wrapped filamentous structures. To me, these “filaments” seem to be much too long and too thin for true tentacles. Since their exact position within the arm crown is difficult to determine, the “filaments” might anyway represent the second dorso-lateral arm pair of a vampyromorph stem-lineage representative.

Apart from these uncertainties, it is even unclear whether those filamentous structures belong to *Mastigophora*. Wilby et al. (2004) have impressively demonstrated the occurrence of very closely associated individuals at Christian Malford. At least two examples show *Mastigophora* and *Belemnotheutis* in a head to head position. It is therefore conceivable that the “filaments” described for *Mastigophora* represents the arm crown of a small *Belemnotheutis* specimen.

Finally, apart from the (non-)existence of true tentacles, the presence of uniserial suckers challenges a classification as Decabrachia, too, and instead clearly supports vampyropod affiliations. Decabrachians are well known to possess bi- or even multiserial longitudinal rows of suckers (Young and Vecchione 1996: 97). In the light of this, it

is worthwhile to note that La Voulte as well as Christian Malford fossils are known to preserve chitinous (or “horny”) structures. Hence, if *Mastigophora* is a decabrachiate, teeth- or hook-bearing rings should have been preserved in close association with the suckers. However, there is no evidence of these structures neither in La Voulte nor in Christian Malford.

Conclusions

Based on the shared presence of very short arms, one pair of near-terminal and ear-shaped fins, and an unusual thickening of the anterior mantle margin, specimen MNHN 74241 from the Lower Callovian of La Voulte is determined as *Mastigophora* aff. *brevipinnis*. A more precise determination is currently hampered by the lack of gladius characteristics as well as significant size differences. *Mastigophora* aff. *brevipinnis* represents the first record of its genus outside the U.K. and therefore slightly extends the biogeographic as well as the stratigraphic distribution. *Mastigophora* aff. *brevipinnis* is classified as a vampyropod mainly due to the presence of uniserial suckers without horny rings and the absence of ventro-lateral tentacles; a phylogenetic relationship with decabrachian coleoids – as suggested by Vecchione et al. (1999) – is hence rejected. As a result, the existence of Mesozoic Teuthida is still unconfirmed.

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