

Morphology and significance of the luminous organs in alepocephaloid fishes

Y. I. SAZONOV

Abstract: Alepocephaloid fishes, or slickheads (two families, Alepocephalidae and Platytroctidae), are deep-sea fishes distributed in all three major oceans at depths of ca. 100-5000 m, usually between ca. 500 and 3000 m. Among about 150 known species, 13 alepocephalid and all (ca. 40) platytroctid species have diverse light organs: 1) postcleithral luminous gland (all platytroctids); it releases a luminescent secretion which presumably startles or blinds predators and allows the fish to escape; 2) relatively large, regular photophores on the head and ventral parts of the body in the alepocephalid *Microphotolepis* and in 6 (of 14) platytroctid genera. These organs may serve for countershading and possibly for giving signals to other individuals of the same species; 3) small "simple" or "secondary" photophores covering the whole body and fins in 5 alepocephalid genera, and a few such structures in 1 platytroctid; these organs may be used for camouflage in the glow of spontaneous bioluminescence; 4) the mental light organ in 2 alepocephalid genera from the abyssal zone (*Bathyprion* and *Mirognathus*) may be used as a lure to attract prey.

Introduction

Alepocephaloid fishes, or slickheads, comprise two families of isospondylous fishes (Platytroctidae and Alepocephalidae). The group is one of the most diverse among oceanic bathypelagic fishes (about 35 genera with 150 species), and these fishes play a significant role in the communities of meso- and bathypelagic animals. Alepocephaloid fishes are widely distributed in all 3 major oceans at depths from ca. 100 to 5000 m, but are most common between 500 and 3000 m; there are no shallow-water species in the group, and it was suggested (MARKLE 1976) that the evolution of all known alepocephaloids had been connected with deep-sea habitats.

Most species belong to engybenthic fishes living usually from several meters to several hundred meters above the bottom over continental and insular slopes, submarine ridges and rises (PARIN and GOLOVAN 1976); many species are often caught in the open ocean over abyssal depths, but all of them have relatively large eggs (2-7 mm in diameter), and a part of their life cycle is no doubt connected with the bottom. Most alepocephaloid species are small (10-15 cm) to medium-sized (15-50 cm) fishes, very rarely larger (up to 1 m). Almost all are darkly coloured (brownish, blackish, dark gray), with few

exceptions (uniformly gray, blue or with darkly coloured body and blue head); the coloration of the body is uniform, with no differences in the colour of the dorsal and ventral parts.

During the period of their evolution in the deep sea, alepocephaloids acquired many adaptations to this particular environment. One group of adaptations connected with the deficiency of light at the depths where these fishes dwell, namely the ability to produce own light (bioluminescence), will be described and discussed below. Bioluminescence is widely distributed in many groups of deep-sea organisms; it is also very common among the deep-sea fishes and there is an extensive literature on this subject (e.g., NICOL 1958, MARSHALL 1960, HERRING and MORIN 1978, YOUNG et al. 1980, KASHKIN 1993). Unfortunately, studies on this aspect of alepocephaloid fishes are quite unsatisfactorily: the external morphology and topography of light organs were used as taxonomic characters (PARR 1951, 1960, MARKLE 1976, 1978, SAZONOV 1976, 1995, MATSUI and ROSENBLATT 1987). Data on the fine structure and functional significance of alepocephaloid light organs are limited (LENDENFELD 1887, NICOL 1958, BEST and BONE 1976, MARKLE 1976, BADCOCK and LARCOMBE 1980). There are also only a few direct observations of bioluminescence in alepocephaloids: only luminescence of the secretion from the platytroctid postcleithral gland were observed (NICOL 1958, SAZONOV unpubl. data).

The purpose of this paper is to present a review of all light organs in alepocephaloid fishes and to discuss their possible significance for these fishes; a mental light organ in two alepocephalid genera is described here for the first time. This paper is based mainly on material published elsewhere; thus, the list of material examined is not presented here. All luminous alepocephaloid species have been examined by the author.

Results and Discussion

The structures for which a luminescent function had been suggested were described relatively early in alepocephaloid fishes (LENDENFELD 1887, BRAUER 1908). In these and many subsequent publications, however, luminous organs were examined in one or few alepocephalid species and the data on the distribution and variability of light organs in the group as a whole are incomplete and scattered in the literature. The following types of luminous organs are known in alepocephaloid fishes: 1) postcleithral luminous gland (and caudal luminous glandules); 2) relatively large, regular, serially arranged photophores; 3) small, irregular or non-serially arranged secondary photo-

phores; 4) mental light organ. None of these luminous organs have been reported to contain luminescent bacteria.

Postcleithral luminous gland ("postclavicular organ", or "shoulder organ")

This gland is characteristic for platytroutids only; all representatives of this family have a paired postcleithral gland, and *Platytroutes apus* also has 2-4 small, unpaired caudal glandules near the dorsal and ventral margin of the caudal peduncle (Fig.1). The postcleithral gland represents a sac-like reservoir (resembling a chemical retort) imbedded in the skin just behind the cleithrum and supracleithrum, with a short external tube supported by a modified scale inside and situated below the lateral line. The walls of the reservoir and tube are intense black (BEEBE 1933). The internal walls of the reservoir consist of a thick layer of dense connective tissue without epithelial covering (probably an artifact), but with a dense population of melanophores and numerous "violet cells" (ca. 5 μm in diameter), which are the precursors of the numerous spherical "red cells" (8 - 40 μm) in the lumen of the gland. The latter are the main component (photogenic bodies) of the luminous secretion released by the gland (NICOL 1958). This author had described the mechanism of luminescence of the postcleithral gland for a small, living individual of *Searsia koefoedi*; the same picture has been observed by the present author for a large specimen of *Holtbyrnia laticauda*. When disturbed, the fish throws out a bright blue-green cloud of its luminous secretion from both postcleithral glands; it shines for 4-5 s, then scatters into multitudinous bright drops and disappears. Repeated stimulations (up to more than 10 times in the case of *H. laticauda*, showed that the light became weaker and intervals between two successful stimulations longer. Light intensity measured for *S. koefoedi* was about 2×10^{-6} mW cm^{-2} at a distance of 1 m in air (NICOL 1958), but in the large *Holtbyrnia* it seemed much more (instrumental measurements were impossible in that cruise). In the latter, the subjective impression was such that one flash could illuminate a small room enough to distinguish printed texts.

The role of the postcleithral gland was already clear to PARR (1951, 1960), who supposed (the paper by NICOL 1958 was unknown to him) that the gland served to release luminescent secretion and was used for passive defence. Sudden blinding of the attacking predator by the bright flash of the luminous secretion helps the fish to leave the site and to escape subsequent attacks. Most probably, the caudal glandules of *Platytroutes* are used for the same purpose: this fish (see Fig.1) is apparently incapable of fast swimming and may use its caudal glands to thwart repeated attack from behind.

Therefore, the postcleithral luminous gland may be recognized as an evolutionary advantage of platytroutids that has no analogy among living teleosts. The luminous caruncles of the deep-sea angler-fishes from the family Ceratiidae weakly resemble this gland (MARSHALL 1960). Surprisingly, a similar mechanism of releasing luminous secretion was found in the deep-sea cephalopod *Heteroteuthis* and in the prawns *Acantheephyra*, *Hoplophorus*, and *Systellaspis* (NICOL 1958, MARSHALL 1960). A more distant analogy can be perceived in the functioning and significance of the ink-sac of shallow-water cephalopods.

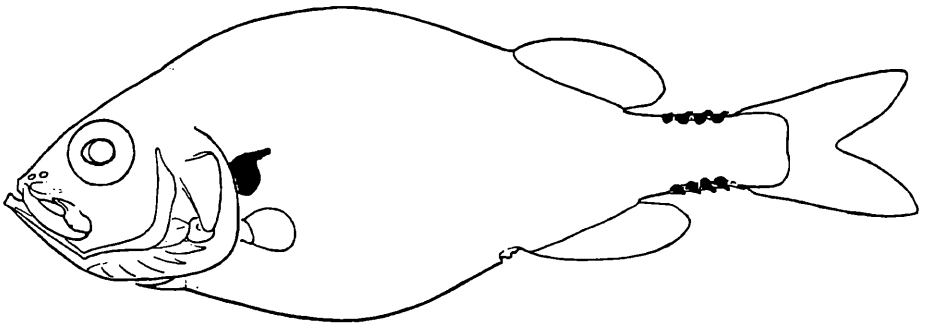


Fig. 1: *Platytroctes apus*. Semi-diagrammatic lateral view showing postcleithral and caudal luminous glands (from PARR 1960, modified).

Regular photophores

Relatively large, variably shaped and developed, but serially arranged structures resembling true photophores of other luminescent fishes (e.g., Myctophidae, Stomiiformes) are found in 6 genera of platytroutids and one genus of alepocephalids; in each group these organs are quite dissimilar and will be described below separately. These organs are under nervous control and all attempts to stimulate them with hydrogen peroxide were unsuccessful (NICOL 1958).

In the family Platytroutidae, regular photophores are developed in the genera *Persparia* (a single species, *P. kopua*), *Holtbyrnia* (in all species except for *H. anomala*), *Sagamichthys* (all 3 species), *Searsia* (a single species, *S. koefoedi*), *Searsioides* (in both of 2 known species), and *Maulisia* (in 2 of 5 species). SAZONOV (1986) suggested that all other platytroutid genera except for *Mentodus* and *Normichthys* have no photophores primarily, whereas in the two latter genera photophores have been secondarily lost. Platytroutid photophores are relatively variable in shape, but the position of each photophore is rather constant (Fig. 2); they are subject to ontogenetic

changes (MATSUI and ROSENBLATT 1971, 1987). The photophore pattern is also a useful taxonomic character to identify genera and species (PARR 1960, SAZONOV 1976, MATSUI and ROSENBLATT 1987, and many others). In general, platytroutid photophores consist of luminescent tissue embedded in the surrounding skin, a lens, and a reflector (only in some photophores on the head); the whole organ has a black lining. The photogenic tissue is red in *Persparsia* and white or yellowish-white in all other genera. Histological data on these light organs are lacking. Most photophores on the head and ventrolateral parts of the body are rounded or semicircular in shape, but usually face downward. Those situated near the midline of the belly are more variable in shape: from rounded to resembling transverse bars, chevrons, or tear-drops; most of them face downward, but some (gular and interventral) face forward and downward. Juveniles of *Persparsia* and *Sagamichthys* have small photophores within the eye-ball (in the iris) that disappear with growth.

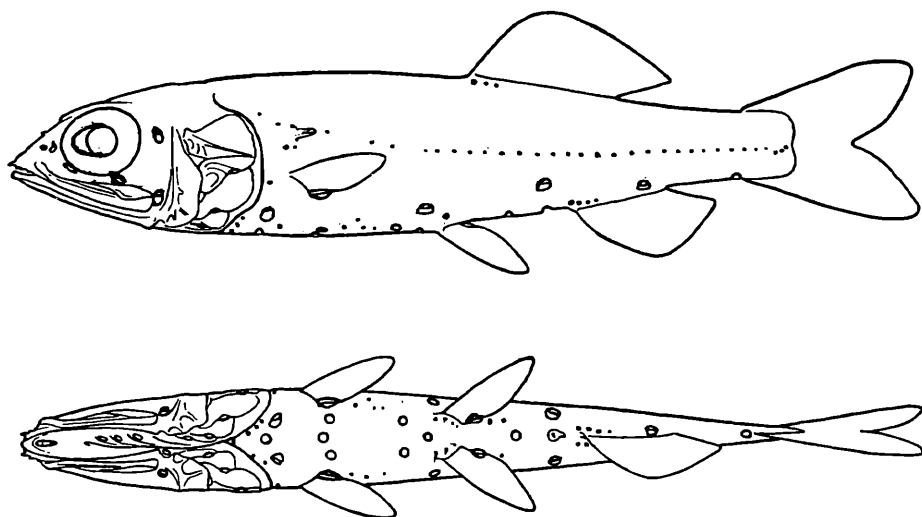


Fig. 2: *Persparsia kopua*. Semi-diagrammatic lateral (above) and ventral (below) views (from PARR 1960, modified) showing photophore pattern.

One more peculiarity connected with the presence of photophores in platytroutids has recently been reported (SAZONOV 1986), namely, a "pineal window" in the skull of those species that have well-developed (and functional) photophores. The pineal window in platytroutids represents an oval space of unpigmented skin on the top of the head over the epiphyseal complex. The latter is stalked and its terminal vesicle penetrates into a deep pit in the chondrocranium close to the transparent frontal bones. As was shown for myctophids inhabiting approximately the same depths as platytroutids, their

pineal complex is more sensitive to light than that in the more shallow-living species (MACNULTY and NAFPAKTITIS 1977). No species without photophores have a pineal window, and one could suppose that this structure is responsible (along with the eyes) for perceiving the light produced by the regular photophores. Moreover, two closely related species of *Maulisia* with poorly developed photophores (*M. mauli* and *M. argipalla*) also differ in this respect: the former has a pineal window, whereas the latter has it already "closed" (overlying skin is densely pigmented) (SAZONOV et al. 1993); the same is true for the species with rudimentary photophores (*H. anomala*).

Regular photophores in *Microphotolepis* (a single species, *M. schmidti*) are rounded structures (up to 0.8 mm in diameter) serially arranged on the body and head beneath the epithelium (and, on the body, also under the scales when the latter are developed). Most of the photophores are located near the ventral parts of the body and head, but they are also numerous on the body sides and near the back (Fig. 3) (SAZONOV 1995). In this species, adults and adolescents also have secondary photophores situated almost over each scale pocket above the scales. These photophores are smaller (see below) and may play a somewhat different role. The histological structure of the regular photophores in *Microphotolepis* were studied by MARKLE (1976), who found them rather similar to secondary photophores of *Rouleina*, with few insignificant differences.

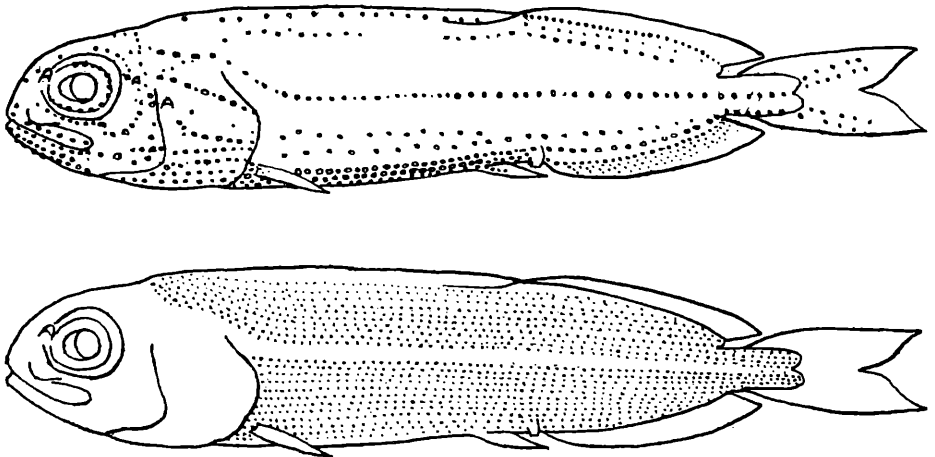


Fig. 3: *Microphotolepis schmidti*. Lateral view of the subadult individual. Above: topography of regular photophores (secondary photophores not shown); below: topography of secondary photophores (from SAZONOV 1995, modified).

An extensive literature exists on the possible significance of regular photophores in fishes (e.g., NICOL 1958, MARSHALL 1960, CLARKE 1963, YOUNG et al. 1980, and many others). However, relatively few species have been experimentally studied in this respect. In spite of this, many hypotheses have been advanced to explain the possible significance of regular photophores, among them doubtful ones prescribing the function of illumination of the fishes' visual field by photophores (MARSHALL 1960) or an illumination of prey by gular photophores in platytroutids (MATSUI and ROSENBLATT 1987). A critical analysis of all the hypotheses proposed is beyond the scope of the present report. Here, only two of them that are more or less applicable to alepocephaloid fishes will be discussed: counterillumination (or countershading) and the utilization of photophores as a signalling device for species recognition.

As shown by CLARKE (1963), the light produced by ventral light organs of mesopelagic fishes "is used as a form of countershading to aid in their concealment from predators". Photophores serve to eliminate the shadowed area that would form on the ventral surface of the fish body in downcoming light. Many mesopelagic stomiiform and myctophiform fish species use their photophores in this manner; the intensity of the luminescence and the wavelength of the emitted light (ca. 475 nm, i.e., blue) are identical with the light of the surroundings. As was shown for some mesopelagic animals (YOUNG et al. 1980), luminescent species can vary the intensity of light emission in connection with the changing intensity of the external light.

However, for alepocephaloids the phenomenon of counterillumination seems insignificant. BADCOCK and LARCOMBE (1980) have pointed out that counterillumination may be used by juvenile *Xenodermichthys copei*, with photophores more numerous near the ventral profile of the body and living near the lower limits of the mesopelagic zone, whereas the adults have photophores distributed more uniformly on the body, dwell deeper, and their photophores may be used for another purpose unknown to the authors (but see below). In this respect, *Microphotolepis* which is usually caught at night at depths of 100-200 m (both juveniles and adults), can probably use its regular photophores for counterillumination along with other migratory mesopelagic fishes (during daytime this species was once recorded from 700 m [BADCOCK and LARCOMBE 1980]). Among platytroutids, only *Perspasia kopua* and juveniles of a few other species (*Sagamichthys abei*, *Holtbyrnia latifrons*) are common above 700 m (MATSUI and ROSENBLATT 1987). In the case of the former species, which belongs to the non-migratory group and is distributed between 200 and 1300 m (usually 400-1000 m), counterillumination might be significant to some extent if the photophores were similar to those in other

mesopelagic fishes, i.e., more numerous and serially arranged along the belly as well as capable of emitting light in the blue part of the spectrum. However, photophores in *Perspersia* are not so numerous, are sparsely set, and red. DENTON et al. (1985) have shown that red light (wavelength 700 nm) scatters and absorbs rapidly at these depths and is already invisible at a distance of a few meters. Therefore, photophores of *Perspersia* cannot serve for counterillumination and must have another purpose. In my opinion, flashes of the photophores in *Perspersia* serve for intraspecific communication at short distances (e.g., within a school), so that these flashes are visible only to these fishes and are invisible to other species. Photophores of other platytroutid species may be used in the same manner, with a single difference: blue light emitted by these organs is visible at a longer distance; the peculiarities of the photophore pattern may serve for distant detection of the species.

"Secondary" photophores ("simple" photophores)

The subdivision of photophores into "regular" and "secondary" seems arbitrary rather than reflecting sufficient differences between both groups, at least in alepocephalids. For example, in 3 alepocephalid genera related to *Microphotolepis* (*Photostylus*, 1 species, *P. pycnopterus*; *Xenodermichthys*, 2 species; *Rouleina*, with 7 luminescent species from a total of 9 known), the head photophores are the homologues of some regular photophores of *Microphotolepis*, but their size and functions are, probably, the same as those of other "secondary" photophores. Only in *Microphotolepis* and *Perspersia* do both the regular and secondary photophores exist. In the former species, secondary photophores (ca. 0.05-0.15 mm in diameter) are situated over almost every body scale (except those in and along the lateral line and on the belly); in the latter species there are a few small organs along the lateral line and somewhere along the bases of the vertical fins, on the belly, and along the lower profile of the caudal peduncle. In *Xenodermichthys*, almost the whole body (it has no scales) is covered with small, nodular photophores (ca. 0.5 mm in diameter; a total of approximately 500) forming rather regular and vertically oblique rows (BADCOCK and LARCOMBE 1980); fewer photophores - similar in shape and size - are located on the head. In most species of *Rouleina*, photophores are similar to those in *Xenodermichthys*, but in *R. maderensis* and *R. livida*, photophores look rudimentary, are less numerous than in other species, and are restricted to the areas near the lower body profile (BRAUER 1906, MARKLE 1978). *Photostylus* has unique and the most unusual photophores among fishes; they are situated on stalks and sparsely set on the head and body (BEEBE 1933, BEST and BONE 1976).

The fine structure of these photophores has been examined by many authors (LENDENFELD 1887, BEST and BONE 1976, MARKLE 1976), but only in a few species (both species of *Xenodermichthys*, *Photostylus*; data on *Microphotolepis* and *Rouleina* are still unpublished). Each photophore contains a connective tissue cup over the pigment layer, with the reflector cup inside and central core cells (which are photogenic) on the surface of the latter cup; the entire organ is covered with epidermis (see BADCOCK and LARCOMBE 1980, Fig.7, p. 288).

The function of secondary photophores was unclear and it has been suggested (BADCOCK and LARCOMBE 1980) that below 500-1000 m these organs cannot be used for counterillumination. Recently, KASHKIN (1993) has hypothesized that "secondary" photophores in fishes may be used for camouflage, too. However, these photophores serve to eliminate shadowed body contours in the glow of spontaneous bioluminescence produced by other luminescent organisms living at these depths; this light is not directed downward and it may explain the distribution of secondary photophores on the whole body of the fish. With increasing depth, the intensity of this bioluminescence becomes less and it disappears or becomes insufficient at depths around 1000-1200 m. However, for some engybenthic species living close to the bottom photophores might retain their significance at these depths, especially with increased abundance and biomass of pelagic animals (bathyal-pelagic biotope according to PARIN and GOLOVAN 1976).

Mental light organ

This probably luminescent organ is described below for the first time. Examination of two monotypic genera from the family Alepocephalidae - *Bathyprion* (*B. danae*) and *Mirognathus* (*M. normani*) - showed that both taxa have a peculiar formation near the tip of the lower jaw. It consists of modified fibers of the anterior portion of the musculus intermandibularis (probably luminescent) and transparent tissues in front of it including the dental bone and interdental cartilage, the anterior end of the ethmoid cartilage and the integument. These transparent tissues may serve as the lenses. The skin covering the head behind this organ as well as the epithelium of the tongue are both darkly pigmented (Fig. 4).

In both genera the eyes are reduced in size; *Bathyprion* has a circumlental pupil. Free neuromasts are extremely abundant on the skin covering the top and sides of the head in front of the eyes. All these features suggest that the organ described above represents a kind of photophore somewhat resembling the gular organ in platytroutids.

B. danae and *M. normani* are known from less than 10 specimens each (most of them were examined by the present author); the majority of these fishes have been collected at depths between 2000-3000 m. Neither sunlight nor spontaneous luminescence can play any role. Populations of deep-sea organisms at these depths are not numerous and food resources are very scarce.

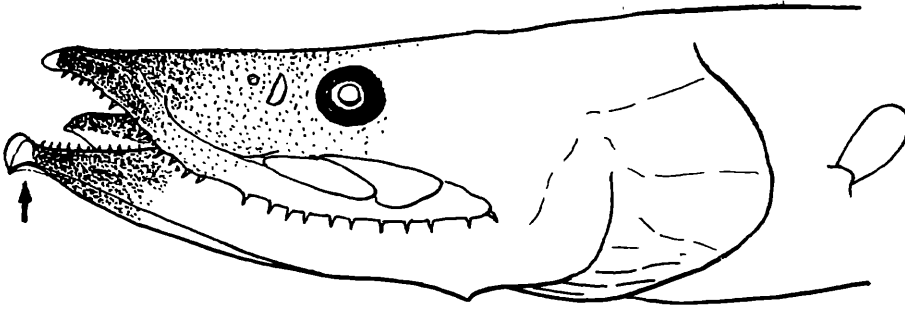


Fig. 4: *Bathyprion danae*. Head, lateral view, showing the position of the mental light organ (after MARSHALL 1966, modified).

In the original description of *B. danae*, MARSHALL (1966) pointed out that "*Bathyprion* may often take its prey at the end of a quite darting movement", taking into account the body shape and consistency of this fish (the mental light organ had not been mentioned by this author), and "*Bathyprion* is more likely to reserve its energies for quick raptorial darts". Such behaviour might seem strange for a fish living so deep if it could not attract its prey. The discovery of the mental light organ, which may be used as a luminescent lure, can explain this method of hunting in *Bathyprion* and *Mirognathus*. The mental photophore in these two genera may represent an adaptation to the scarcity of food.

Summary

Like many other deep-sea organisms, alepocephaloid fishes have light organs acquired independently in several lineages. These organs are unlike photophores in other taxa of deep-sea fishes and were developed convergently with them as adaptations to the scarcity of light and, in one case, of food at meso- and bathypelagic depths. The significance of these organs for alepocephaloids, however, is the same as for other deep-sea fishes: they serve for passive defence (blinding the predator, camouflage), as communication signals to other individuals, and to attract prey.

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Address of the author:

Yuri I. SAZONOV, Zoological Museum of the Moscow Lomonosov State University, Bolshaya Nikitskaya 6, Moscow K-9, Russia.

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