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Author(s): Hugo Gevaerts, Jozef B. Moens, Els E. Martens and Ernest R. Schockaert

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Hard parts in the female system of *Syndesmis longicanalis* (Platyhelminthes, Rhabdocoela, Umagillidae) are basement membrane derivatives

Hugo Gevaerts¹, Jozef B. Moens¹, Els E. Martens²,
and Ernest R. Schockaert¹

¹ Zoology Research Group, Dept. SBG, Limburgs Universitair Centrum, B-3590 Diepenbeek, Belgium

² Dept. of Zoology, University of Nairobi, P.O. Box 30197, Nairobi, Kenya

Abstract. Data are presented on the ultrastructure of the sclerotised parts in the female system of the symbiotic turbellarian (Platyhelminthes) *Syndesmis longicanalis*. The bursal canal, insemination canal, and bursal valve are basement membrane derivatives. These structures are compared with hard parts derived from basement membrane in other turbellarians. The taxonomic value of the bursal valve in Umagillidae is rejected.

Additional key words: symbiotic turbellarians, bursal valve

Hard or so-called “sclerotic” elements in Platyhelminthes have generally been revealed to be intracellular derivatives, presumably of actin nature (Cohen et al. 1982): the oncospherical hooks of Cestoda (Swiderski 1973), the spines in the cirrus of *Fasciola hepatica* (Threadgold 1975), and the hard parts of the copulatory organ in the majority of platyhelminth taxa such as Haplopharyngida (Doe 1986), most families of the Proseriata (Ehlers & Ehlers 1980; Martens 1986) and the Rhabdocoela (Brüggemann 1986). Also the “bursal mouthpiece” of the acoel *Philocelis cellata* appears to consist of intracellular condensations in stacked cells (Brüggemann 1985). So far two exceptions have been found: the proboscis teeth and hooks in the Schizorhynchia (Kalyptorhynchia)—*Carcharodorhynchus* sp., *Diascorhynchus* sp. (Rieger & Doe 1975), and *Cheliplana* sp. (Doe 1976)—on the one hand, and the stylet and spines of the cirrus of representatives of the proseriate family Monocelididae (Martens & Schockaert 1981; Martens 1984, 1986) on the other hand.

Hard parts in the female system of turbellarians other than *Philocelis cellulata* have not been investigated on the ultrastructural level so far. Data presented below on the bursal canal, insemination canal, and bursal valve of the symbiotic rhabdocoel *Syndesmis longicanalis* MOENS ET AL. 1994 show that the sclerotic parts in the female system are basement membrane derivatives.

The taxonomy of the *Syndesmis-Syndisyrix* species complex has been discussed by several authors and the validity of the genus *Syndisyrix* LEHMAN 1946 has repeatedly been questioned (see discussion in Moens

et al. 1994). The so-called bursal valve being a central topic in this discussion, some conclusions on the taxonomic value of this character can be drawn from our observations.

Methods

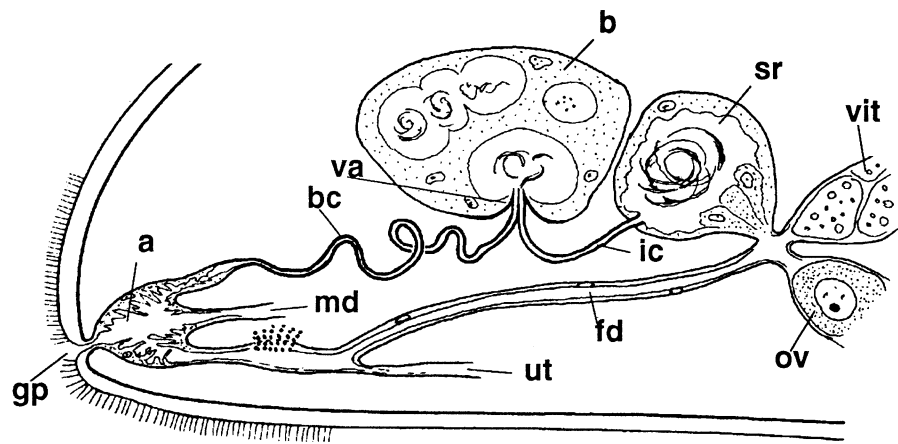
Specimens of *Syndesmis longicanalis* MOENS ET AL. 1994 were collected from the intestine of the sea urchins *Tripneustes gratilla* LINNAEUS 1758 and *Toxopneustes pileolus* LAMARCK 1816 from the Kenyan coast near Mombasa. After light-microscopic (LM) examination, some specimens were fixed in Bouin's for paraffin sections and stained with the modified Mallory method (Fuchsin, Anilin blue, Orange G, modified after Cason in Romeis 1968); other specimens were fixed in 2.5% glutaraldehyde in 0.1 M cacodylate buffer, postfixed in cacodylate-buffered 1% osmium tetroxide, dehydrated in an acetone series, and embedded in araldite. Semi-thin and ultrathin sections were made with a Reichert ultramicrotome. Semi-thin sections were stained with thionine methylene blue, while ultrathin sections were stained with uranyl acetate and lead citrate for transmission electron microscopy (TEM) and observed with a Phillips 300 TEM.

Results

Light microscopic observations

The female atrial organs of *Syndesmis longicanalis* consist of a bursal canal leading from the atrium to the bursa, and an insemination canal connecting the bursa to the seminal receptacle (Fig. 1). At the atrial

Fig. 1. Diagrammatic reconstruction seen from the right of the relevant female organs in *Syndesmis longicanalis*. Atrium (a), bursa (b), bursal canal (bc), insemination canal (ic), female duct (fd), genital pore (gp), male duct (md), left ovary (ov), seminal receptacle (sr), uterus (ut), bursal valve (va), left vitellarium (vit). Right ovary and right vitellarium not shown.



end the bursal canal is slightly funnel-shaped. The bursal and insemination canals are contiguous for a short distance before opening into the bursal cavity in a region which may be raised as a nipple-like flange above the bursal surface. This region is known as the bursal valve (Lehman 1946).

The canals, the valve, and the wall of the broadened atrial part of the bursal canal form the so-called "sclerotic" or hard parts of the female system (often erroneously referred to as "cuticular"). They are clearly visible in the living animal and in whole mounts. In light-microscopic sections, stained with Mallory's triple stain, they show the same stain reaction as the basement membrane under the epidermis, which is clearly distinct from the reaction of the stylet of the copulatory organ, presumably of intracellular origin.

Ultrastructure

The bursal valve is thickest (about 0.5 μm) at the point where it surrounds the ends of the canals in the bursa (Figs. 2, 5, 7) and becomes gradually thinner towards the outside of the "nipple" (Fig. 3) where it is continuous with the basement membrane around the bursa (Fig. 4). It is clear that the valve is derived from the basement membrane of the bursal epithelium in which the middle layer has become considerably thickened. The valve has a trilamellar structure (Fig. 6): a thin apical electron-dense layer of 20 nm at the bursal (epithelial) side, an electron-dense middle layer of densely packed material (with an outer less electron-dense zone of about 25 nm), and a basal loose fibrous layer of moderate electron density of about 100 nm. At the point of maximal thickness the middle layer can be over 300 nm. Where this middle layer is very thick a pattern of meandering more electron-dense lines and less electron-dense spherules can be seen (Fig. 5). At the bursal side it is covered by epithelial cells, which become very thin and eventually disappear towards the

exit of both the bursal canal and the insemination canal (Figs. 5, 7). Muscle fibres are attached to the basal layer by hemidesmosomes (Fig. 3). These fibres run parallel with the contiguous regions of both canals.

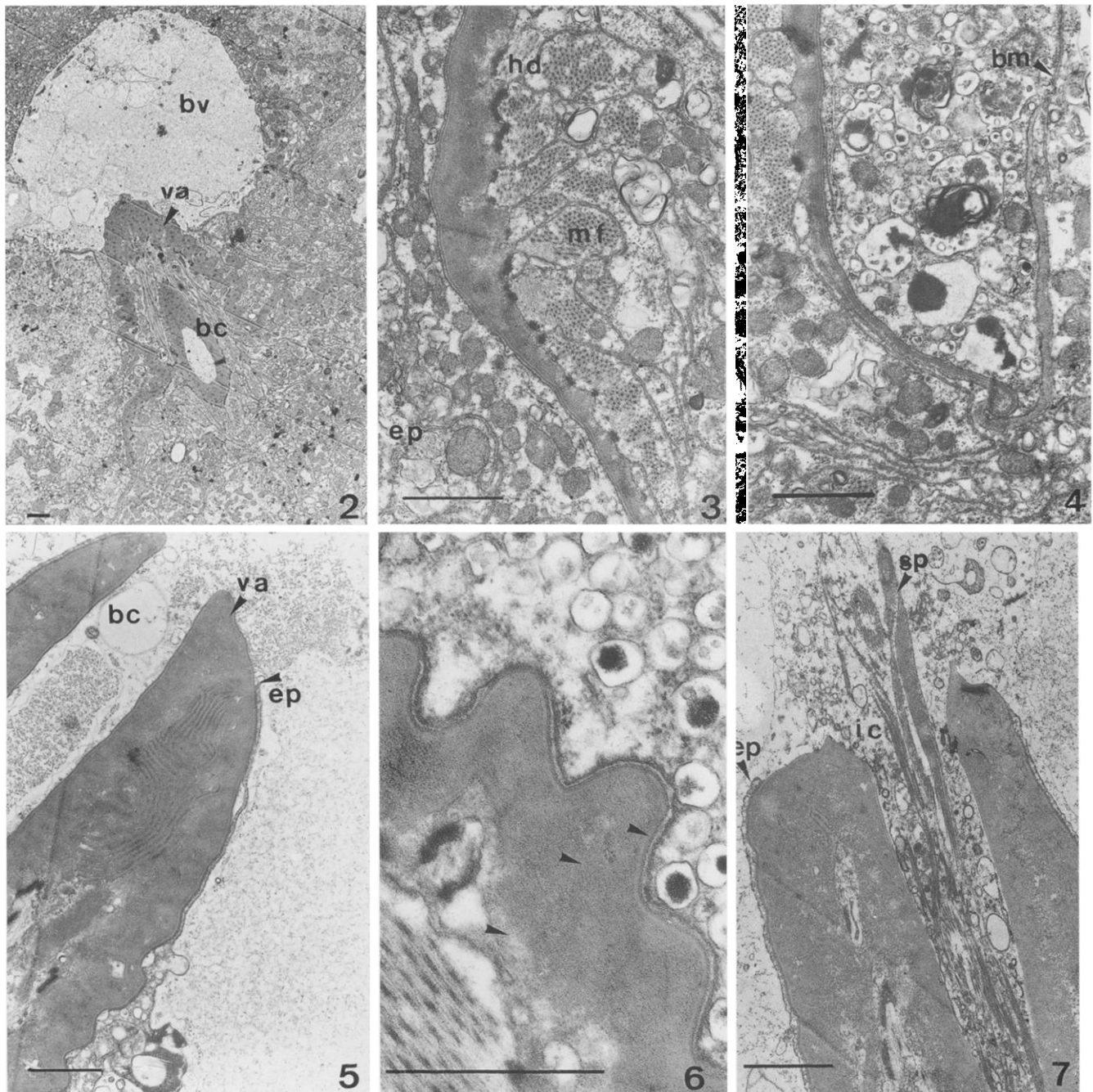
The walls of the insemination and bursal canals consist of the same three layers (about 0.5 μm thick) (Figs. 8–10), continuous with those of the valve (Figs. 5, 7) and similarly derived from basement membrane. No epithelial cells line the canals but cellular remnants can be seen in the lumen of the bursal canal (Figs. 8, 9). Epithelial cells are still present in the first part of the bursal canal, near its origin at the atrium where they have long, irregular lamellae (Figs. 11, 12) as do the epithelial cells of the atrium itself. The basement membrane becomes gradually thicker from the funnel-shaped connection with the atrium towards the canal.

The bursal and insemination canals are each about 2.5 μm in diameter. They are surrounded by longitudinal muscles that are attached to the basement membrane with hemidesmosomes as at the bursal valve (Figs. 8–10).

In the bursa, large irregular cells surround a number of cavities containing cell remnants and clusters of sperm (Fig. 2). The cytoplasm of these cells contains numerous small vesicles (many with an electron-dense core), larger vesicles, and multivesicular bodies (see Figs. 3, 4, 6). One such cavity between bursal cells is invariably located at the opening of the canals. Bundles of sperm enter the insemination canal, in the lumen of which cross sections of sperm can be recognised (Figs. 7, 10). Sperm appear to have the same structure as described in *Syndisyrix punicea* (HICKMAN 1956) by Rohde & Watson (1988).

Discussion

From the description above it is apparent that the bursal valve and the walls of the bursal and insemination canals are basement membrane derivatives.



Figs. 2–7. Bursal valve in *Syndesmis longicanalis*. TEM. Scale bars, 1 μ m.

Fig. 2. Low magnification of the valve (va) and a section of the bursal canal (bc), showing the nipple-like appearance of the valve protruding in a vesicle (bv) in the bursa.

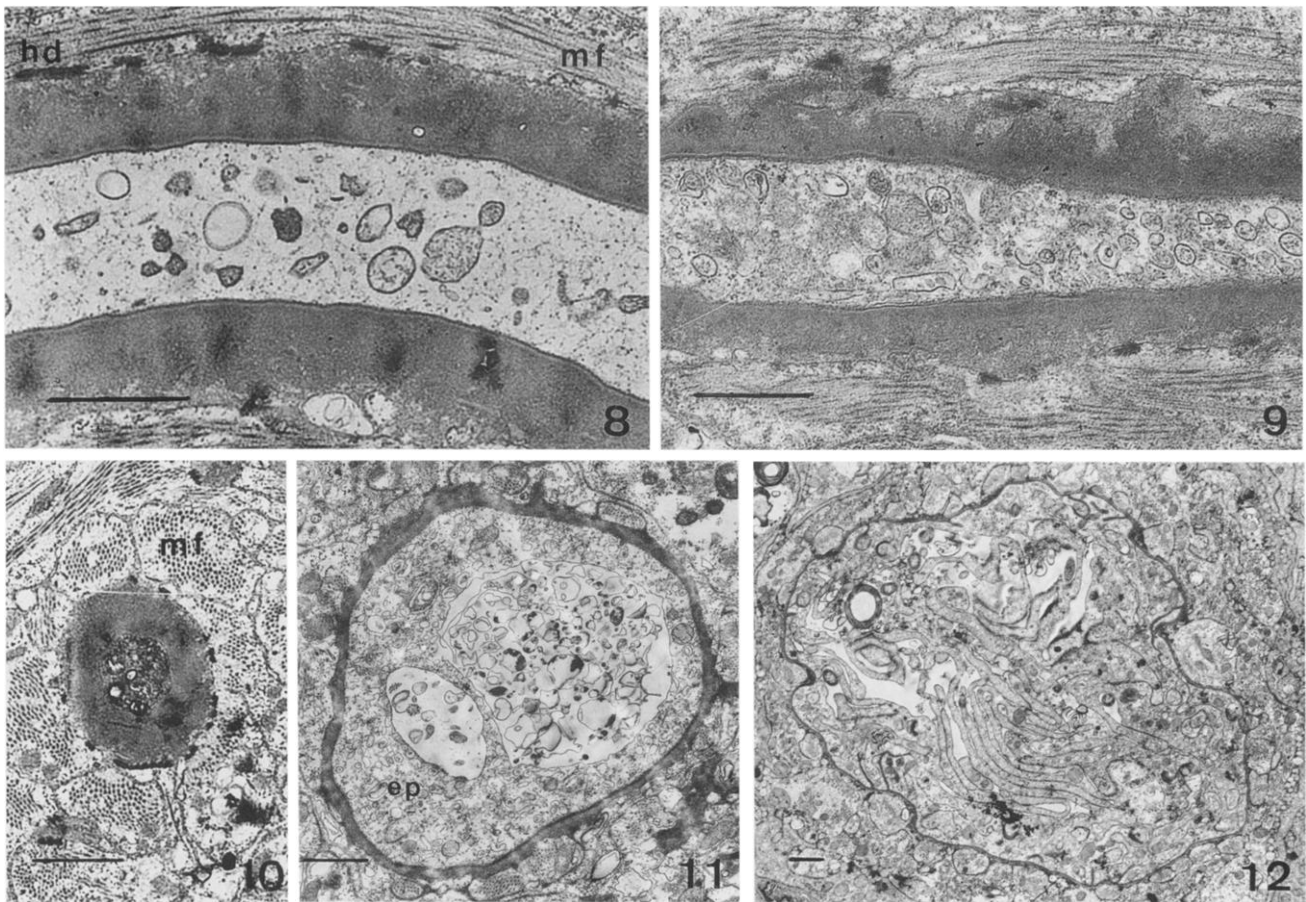
Fig. 3. Section through the bursal valve; top closest to the canals. Note the appearance of the epithelium (ep) at the bursal side and the muscles (mf) attached by hemidesmosomes (hd) to the valve.

Fig. 4. The outermost region of the valve (top left closest to the canals) showing that the valve becomes thinner and gradually merges into the basement membrane (bm) of the epithelium in the bursa.

Fig. 5. Transition of the valve (va) into the wall of the bursal canal (bc) showing the meandering structure and spherules in the thick middle layer and the thin covering epithelium (ep) that ends near the entrance of the bursal canal.

Fig. 6. Higher magnification of the valve showing the three layers of which it consists (epithelium on the right).

Fig. 7. Opening of the insemination canal (ic) and the continuity with the valve. Note sperm (sp) partly within the canal and the termination of the epithelium (ep) that covers the bursal valve.



Figs. 8–12. Canals and atrium in *Syndesmis longicanalis*. TEM. Scale bars, 1 μm .

Fig. 8. Longitudinal section through the bursal canal of an adult individual. Note the cell remnants in the lumen and the trilamellar appearance of the wall. The longitudinal muscles (mf) surrounding the canal are attached to its wall by hemidesmosomes (hd).

Fig. 9. Longitudinal section through the bursal canal in a presumably younger individual. The cell remnants of the epithelium are less degenerated and middle layer in the wall is less dense and with an irregular outer aspect compared to that in Fig. 8.

Fig. 10. Cross section through the insemination canal that is surrounded by longitudinal muscle fibres (mf). The lumen is filled with sperm.

Figs. 11, 12. Cross sections through the bursal canal near the atrium, the section in Fig. 12 closest to the atrium. Note the presence of the epithelium (ep) with indications of degeneration in Fig. 11 and with lamellar expansions in Fig. 12. The thickness of the basement membrane decreases towards the atrium.

That so-called “sclerotic” elements can in fact be derivatives of the basement membrane has been shown: spines and hooks on the proboscis of some Kalyptorhynchia (Rieger & Doe 1975), stylets and cirrus spines in the copulatory organ of the Monocelididae (Martens & Schockaert 1981; Martens 1984, 1986). It is therefore not surprising that hard parts in the female system of Platyhelminthes can also be derived from basement membrane. Rieger & Doe (1975) and Rieger (1981) pointed out that in the absence of “true” cuticular formations in Platyhelminthes, sclerotic parts can differentiate only from intracellular components (such as the

terminal web: Rieger 1981) or from extracellular matrix (such as the basement membrane). Intracellular hard parts probably will be found in the female system of some Platyhelminthes and other species are now under investigation.

The trilamellar structure seen in the wall of the bursal and insemination canals and the thicker part of the bursal valve corresponds to that observed in the Schizorhynchia and in the Monocelididae. An electron-dense layer beneath the epithelium is invariably present (20–50 nm thick), a middle slightly less electron-dense layer of variable thickness, and a layer of 100–

400 nm of a finely fibrous material towards the muscles. In all species studied so far it is the middle layer that grows thicker and may show a heterogeneous aspect : (1) with small irregular less electron-dense spherules as in the stylet of *Monocelis fusca*, in the basal part of the stylet of the prostatoid organ of *Ectocotyla multitesticulata* (Martens 1986, figs. 4, 11), and in the thickest part of the bursal valve in *Syndesmis* (Fig. 5); (2) with a "floculate" appearance as in the stylet of the prostatoid organ of *E. multitesticulata* (Martens 1986, figs. 7–9); or (3) with a meandering structure as in *Syndesmis longicanalis* (Fig. 5). In *Chepliiana* sp. there are a number of hollow tubes within this middle layer (Doe 1976, p. 106, figs. 2A,D). The slightly less electron-dense zone within this middle layer towards the epithelium may be absent (or at least inconspicuous) or present in variable thickness. Collagenase applied to thin sections causes the spines in the cirrus of Monocelididae to disappear (E. Martens, unpubl. data), indicating that they are probably made of collagenous material that may be condensed or organised (even chemically) in different ways.

The epithelium that covers the (thickened) basement membrane may remain, as on the spines in the proboscis of *Carcharodorhynchus* sp. (Rieger & Doe 1975) or within the stylet of *Archilopsis* sp. (Martens 1986), often showing stacked membranes, and in *Syndesmis longicanalis* on the bursal valve. Alternatively, the epithelium may disappear in the adult stage, as in the cirrus of Monocelididae and in the bursal and insemination canals of *Syndesmis*, leaving behind cell debris of the degenerated epithelium (Figs. 8, 9).

The basement membrane origin vs. intracellular formation of the hard parts in turbellarians has been used to formulate hypotheses on the phylogenetic relationships of the taxa studied. Intracellular formation of the hard parts of the copulatory organ is considered to be the plesiomorphic situation in Platyhelminthes (Martens 1984; Brüggeman 1986). Hence Martens (1984) concluded that the basement membrane origin of the cirrus spines can be considered a synapomorphy for the Monocelididae (whereas hard parts of the copulatory organ in other Proseriata are of intracellular origin). The fact that teeth and hooks on the proboscis of the Schizorhynchia are basement membrane derivatives supports, according to Doe (1976), the view that the Schizorhynchia is a monophyletic taxon (implying that the intracellular formation of hooks in some of the Eukalyptorhynchia represents the plesiomorphic condition). The distribution of the two ways of formation of hard parts in the female systems of Platyhelminthes is yet to be investigated.

Major importance has been attributed to the presence or absence of the bursal valve for taxonomy with-

in the Umagillidae. The presence of this valve was indeed the basis for the erection of the genus *Syndisyrix* by Lehman (1946). The validity of this character has been questioned (Marcus 1949; Stunkard & Corliss 1951; Moens et al. 1994) and the taxonomy of the *Syndesmis-Syndisyrix* species complex has become very confused. The bursal valve is nothing but a thickened basement membrane, a mere continuation of the wall of the canals, and it may be more or less visible under the light microscope depending on the degree of development (even in a specimen that appears "adult"). The "nipple-like" appearance of the valve also may be more or less conspicuous, possibly depending on the state of contraction or relaxation of the muscles attached to it. Because of these inconsistencies, presence or absence of a bursal valve in Umagillidae is not a reliable character and should not be used in the taxonomy.

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