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A NEW SPECIES OF *TRITONIA* (OPISTHOBRANCHIA: GASTROPODA) FROM THE CARIBBEAN SEA

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ABSTRACT

The tritoniid opisthobranchs of the western Atlantic have recently been reviewed (Marcus, 1983). Seven species in three or four genera are known from tropical and subtropical waters of the region. Investigations by one of us (M.T.G.) in the Bahamas yielded specimens of what appeared to be an undescribed species of *Tritonia*. Subsequently, our joint investigations in Quintana Roo, Mexico have provided additional specimens of this species. This paper describes the anatomy of this new species and compares it to closely allied species.

DESCRIPTION

Tritonia hamnerorum new species

Type Material.—Holotype: Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, CASIZ 061278, near La Ceiba Hotel, Puerto Morelos, Quintana Roo, Mexico, on *Gorgonia flabellum* Linnaeus, 2 m depth, 27 March 1985, collected by T. M. Gosliner.

Paratypes.—CASIZ 061279, 87 specimens, near La Ceiba Hotel, Puerto Morelos, Quintana Roo, Mexico, on *Gorgonia flabellum*, 2 m depth, 27 March 1985, collected by T. M. Gosliner.

Paratypes.—CASIZ 061280, 14 specimens, Sandy Cay, Great Abaco Island, Bahamas, on *Gorgonia flabellum*, 4 m depth, 16 July 1983, collected by M. T. Ghiselin.

Etymology.—This species is named for William and Peggy Hamner, who accompanied one of us (M.T.G.) while collecting the specimens in the Bahamas.

External Morphology.—The living animals (Figure 1) reach 15 mm in length. The notum is smooth, devoid of tubercles. The ground color of living specimens is light pinkish purple, the same color as their gorgonian prey. Extending the length of the notum are a series of approximately 20 opaque white longitudinal lines. The lines are irregular with some short interconnecting lines. The gills, rhinophores and velar tentacles are tipped with opaque white. The preserved specimens (Fig. 2) reach 11 mm in length. The semi-circular velum (Fig. 3) contains 2–3 pairs of velar tentacles, including the outermost, which are the oral tentacles. In some cases there are only two tentacles on one side and three on the other. The rhinophores (Fig. 4) contain a series of simple or slightly pinnate digitiform lobes, surrounding the cylindrical apical papilla. In five specimens examined there are nine slightly pinnate gills (Figs. 2, 5) on each side of the body. There are 5–7 irregular lobes on the rhinophore sheath. The outer lobe is largest and triangular in shape. The anus (Fig. 2) is situated between the third and fourth gills, on the right side of body, ventral to the notal brim. The nephroproct is immediately dorsal to the anus. The distinct male and female gonopores, located between the first and second gills, below the notal brim, are well separated from each other. The anterior end of the foot is simply rounded.

Digestive System.—The buccal mass is thick and muscular. Well developed oral glands surround the dorsal, lateral and ventral surfaces of the buccal mass. The jaws (Fig. 6) are thin and elongate with a long masticatory border, consisting of about six rows of acutely pointed denticles. The radula (Figs. 7–9) has a formula

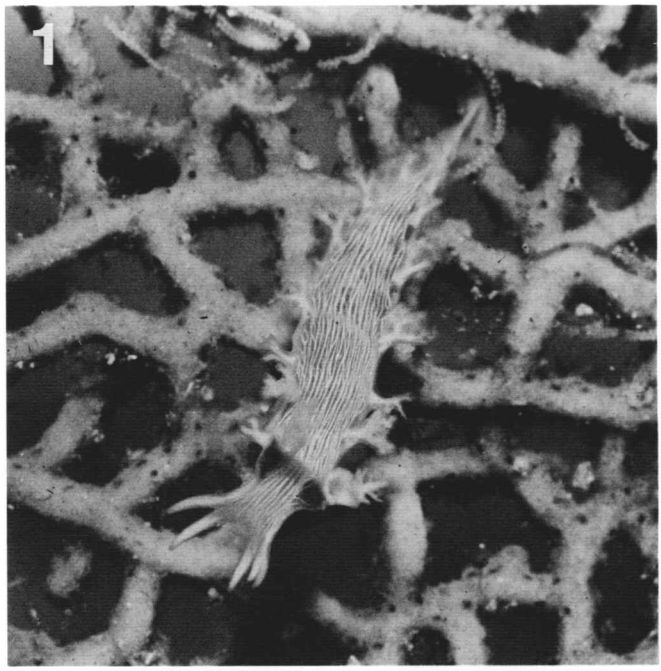


Figure 1. *Tritonia hamnerorum* new species. Living animal.

of 26–29 × 9–10.1.1.1.9–10., in three specimens examined. The rachidian teeth are tricuspid with an acute central cusp, which is often worn in older teeth. The lateral denticles of the rachidian are broadly triangular. The inner lateral teeth are hook-shaped, with an inner denticle. Their anterior surface bears 5–8 irregularly spaced denticles. In older teeth these denticles may not be present, due to wear. The outer lateral teeth are sickle shaped and become progressively more elongate towards the outer margin. The elongate and strap-like salivary glands join the buccal mass at the junction of the esophagus and buccal mass. The esophagus is narrow, but expands into the stomach as it enters the digestive gland. There are no cuticular plates or ridges within the stomach.

Central Nervous System (Fig. 10).—All of the ganglia form a mass on the dorsal surface of the esophagus and buccal mass. The cerebral ganglia are completely fused with the pleurals, and are closely appressed to each other. The pedal ganglia are separated by a short commissure. The buccal ganglia are ventral to the pedal ganglia and are closely appressed to each other. They are situated at the ventral surface of the junction of the esophagus with the buccal mass.

Reproductive System (Fig. 11).—The preampullar coelomic gonoduct is narrow and expands into the short, saccate ampulla. The ampulla again narrows into the postampullar gonoduct. After a short distance the gonoduct branches into a short, narrow oviduct and a thicker, non-prostatic vas deferens. The oviduct enters the female gland mass near the albumen gland. The small membrane gland is adjacent and distal to the albumen gland. The large mucous gland makes up the bulk of the reproductive system. The receptaculum seminis is spherical and muscular. It joins the mucous gland at the female aperture by means of a narrow duct of moderate length. The non-prostatic vas deferens widens into a prostatic portion,

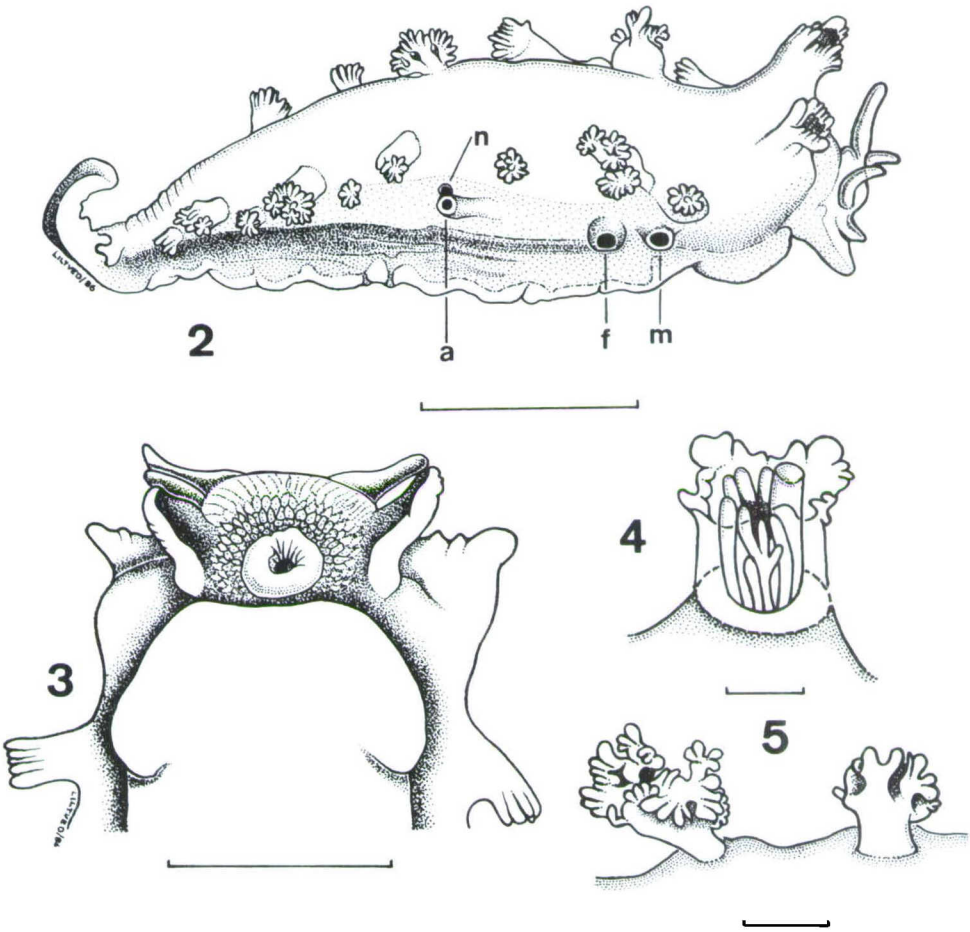


Figure 2. *Tritonia hamnerorum* new species. Right lateral view of preserved animal; a = anus, f = female aperture, m = male aperture, n = nephroproct; scale = 2.0 mm.

Figure 3. *Tritonia hamnerorum* new species. Ventral view of head, scale = 1.0 mm.

Figure 4. *Tritonia hamnerorum* new species. Rhinophore, scale = 0.25 mm.

Figure 5. *Tritonia hamnerorum* new species. Gill, scale = 0.25 mm.

which enters the proximal end of the penial sac. The short, rounded penial papilla is unarmed, and is contained in a conical penis sac.

Egg Mass.—The egg mass, also visible in Figure 1, is a white convoluted ribbon that is closely appressed to the surface of the gorgonian colony. There is a single egg per capsule. Because the veligers have a well-developed velum, they are likely to be planktotrophic. The larval shell is type 1 (Thompson, 1961).

Natural History.—Specimens have been found only in association with the gorgonian, *Gorgonia flabellum* Linnaeus. In the Bahamas specimens were found on an attached gorgonian, while the animals from Mexico were found on a detached, but still living, colony. There were 88 individuals of *Tritonia hamnerorum* present on the single sea fan found in Mexico.

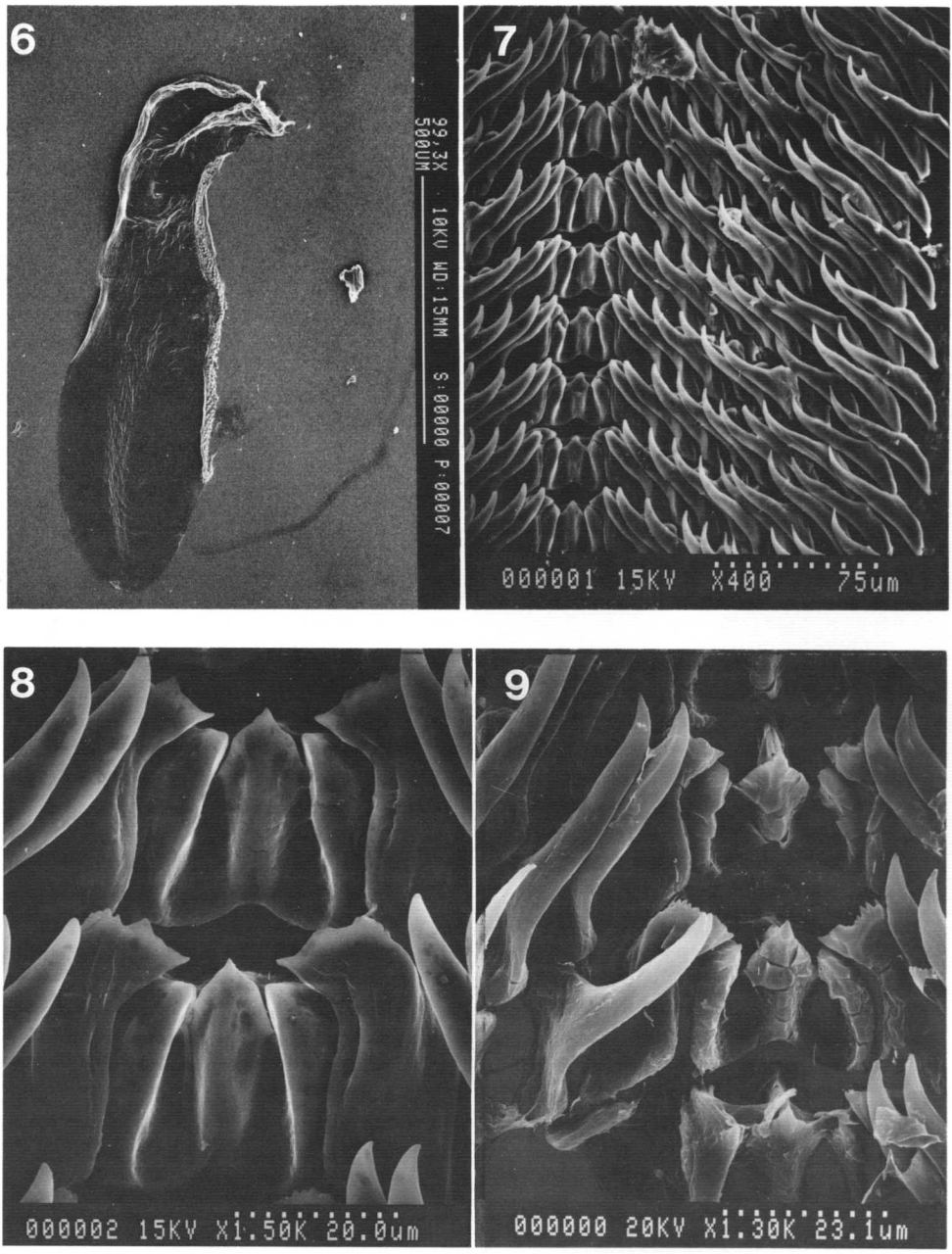
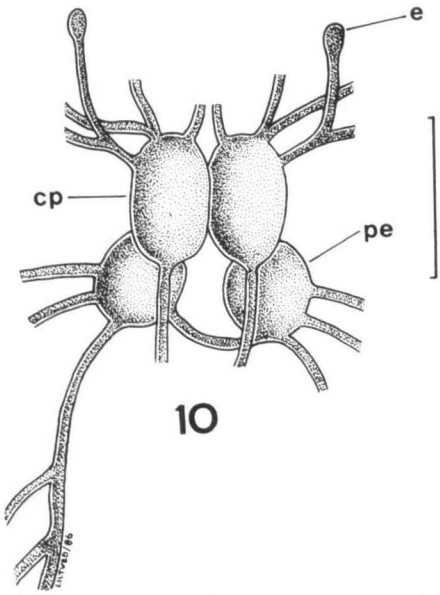


Figure 6. *Tritonia hamnerorum* new species. Scanning electron micrograph of jaw.

Figures 7–9. *Tritonia hamnerorum* new species. Scanning electron micrographs of radula.



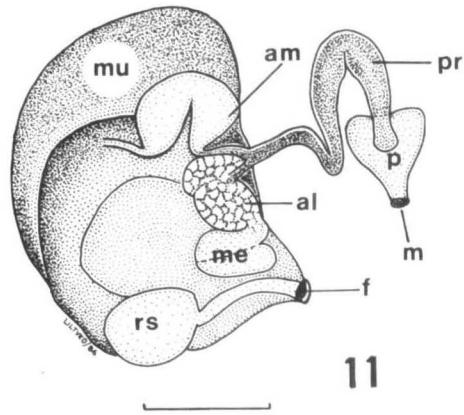


Figure 10. *Tritonia hamnerorum* new species. Central nervous system; cp = cerebral pleural ganglion, e = eye, pe = pedal ganglion; scale = 0.5 mm.

Figure 11. *Tritonia hamnerorum* new species. Reproductive system; al = albumen gland, am = ampulla, f = female aperture, m = male aperture, me = membrane gland, mu = mucous gland, p = penis, pr = prostate, rs = receptaculum seminis; scale = 0.5 mm.

Discussion

The separation of genera within the Tritoniidae has long been the subject of controversy (Eliot, 1905; Odhner, 1926; 1963; Marcus, 1983). A variety of characters have been employed to separate genera, including shape of the rachidian radular tooth, presence or absence of chitinous plates in the stomach, division of the liver (digestive gland), position of the anus, gonopore and nephropore, and shape of the penis.

Odhner (1963) attempted to clarify the systematic arrangement of genera in the Tritoniidae. He considered 8 genera with 4 subgenera of *Tritonia.* Marcus (1983) noted difficulties in clearly differentiating genera. Part of the problem is that different authors have utilized different characters to distinguish genera. Odhner (1963) emphasized that species of *Tritoniella* are characterized by digitiform processes rather than branched gills along the edge of the notum and have a mid-dorsal ridge. Species in this genus have an annulation on the tip of the penis. Marcus (1983) included all tritoniids with an annulation around the penis in the genus *Tritoniella,* including *Tritonia festiva* (Stearns, 1873) and *T. episcopalis* Bouchet, 1977. *Tritonia diomedea* Bergh, 1894, also has an annulation near the apex of its penis (Thompson, 1971, present study). These species have well developed gills and lack a mid-dorsal ridge. It is likely that the presence of a penial annulation is due to parallel evolution of this structure in *Tritoniella* and in some members of *Tritonia.*

Odhner (1963) distinguished *Duvaucelia* from *Tritonia* on the basis of the position of the genital aperture and anus. However, *Tritonia hamnerorum* new species and *T. striata* Haefelfinger, 1963 share characteristics of both genera. The anus is in the anterior half of the body (as in *Duvaucelia*) while the gonopores are

posterior to the anteriormost gills (as in *Tritonia*). Thus the separation of *Tritonia* and *Duvaucelia* cannot be maintained. The splitting of *Tritonia* into subgenera as advocated by Odhner (1963) is not supported by distinct morphological gaps or readily apparent monophyletic groups. Whether the penis is conical or flagelliform has to be evaluated subjectively and varies considerably within and between species (Thompson, 1971; Marcus, 1983). Similarly, the form of the velum (bilobed or entire) and the notum (smooth or with small tubercles) varies between individuals of the same species and is correlated with fixation. Therefore, distinctions between subgenera are artificial and unnecessary.

All species of tritoniids with well developed gills, a tricuspid rachidian tooth and without stomach plates are here considered as members of *Tritonia.* This genus includes large, broad-bodied species such as *T. hombergi* Cuvier, 1798 (Thompson and Brown, 1984) and small graceful species like *T. pickensi* Marcus and Marcus, 1967. Within the genus, species may have a broad radula (as in *T. eriosi* Marcus 1983, which has 160 lateral teeth per half row) or a narrow one (as in *T. hamnerorum,* which has 9–10 laterals (present study)). The shape of the penis, position of the anus and gonopore vary, as discussed above.

Tritonia hamnerorum differs significantly from all previously described members of the genus. The coloration of the living animal clearly distinguishes it from other species. Several other species are known to possess opaque white pigment on the notum. *Tritonia lineata* Alder and Hancock, 1848 has two undulating white lines along the margins of the notum with a branch to each gill (Thompson and Brown, 1984). In *T. bayeri* Marcus and Marcus, 1967, there is an elaborate network of opaque white lines. *Tritonia festiva* (Stearns, 1873) has a series of two or three white marginal lines and several ovals in the center of the notum (MacFarland, 1966, present study). *Tritonia pickensi* Marcus and Marcus, 1967 has a large middorsal patch of opaque white on its notum (Bertsch and Gosliner, 1984). *Tritonia hamnerorum* is the only species that is known to possess a series of approximately 20 longitudinal lines.

Several other aspects of the morphology of *T. hamnerorum* distinguish it from other members of the genus. *Tritonia hamnerorum* is compared with the 13 other species of *Tritonia* that are known from the Atlantic Ocean (Table 1). Of these species, only *T. hamnerorum* and the two other Caribbean species, *T. wellsi* Marcus, 1961 and *T. bayeri* Marcus and Marcus, 1967, possess a fleshy extension on the outer side of the rhinophore sheath. *Tritonia hamnerorum* appears to be unique among described tritoniids in that there are distinct, well-separated male and female gonopores.

Internally, there are several other features that distinguish *Tritonia hamnerorum* from other members of the genus. Several other species are known to possess denticles on the surface of the inner lateral teeth. In *T. plebeia* and *T. hombergi* denticles are present on the inner lateral tooth of juveniles, but are absent in adults (Thompson and Brown, 1984). In *T. australis* (Bergh, 1898) and *T. nilsodhneri* (Marcus, 1983) a single denticle may be present on the innermost lateral. *Tritonia wellsi* Marcus, 1961, *T. pickensi* Marcus and Marcus, 1967, *T. bayeri* Marcus and Marcus, 1967 and *T. hamnerorum* all have several denticles on the inner lateral tooth in adult animals. In *T. bayeri* and *T. wellsi* there are also denticles on the second lateral, while in *T. pickensi* and *T. hamnerorum* the second laterals are always smooth. These four species are also similar in that they have appendages on the rhinophore sheaths and a narrow radula with few lateral teeth.

The four species differ significantly in their reproductive morphology. *Tritonia pickensi* and *T. wellsi* have an elongate penial papilla, while it is short and conical in *T. bayeri* and short and rounded in *T. hamnerorum.*

Table 1. Morphological variability in Atlantic *Tritonia*

Species	Rhinophore sheath	Velar tentacles	Gonopore	Radular formula
australis	with series of short lobes	6–10	single ventral to 6th gill	40–44 × 44–50.1.1.1.44–50
bayeri	with single elongate appendage	4–6	single between 2nd and 3rd gills	20–34 × 9–10.1.1.1.9–10
challengeriana	smooth	8–20	—	32–43 × 30–45.1.1.1.30–45
episcopalis	smooth	11	single ventral to 2nd gill	53 × 74.1.1.1.74
eriosi	with denticulate appendage	16	single ventral to 3rd gill	100 × 160.1.1.1.160
griegi	smooth	10–13	single ventral to 4th gill	48 × 98.1.1.1.98
hamnerorum	with triangular outer lobes and smaller inner lobes	4–6	double between 1st and 2nd gills	26–29 × 9–10.1.1.1.9–10
hombergi	smooth	up to 40	single —	maximum 73 × 229.1.1.1.229
manicata	smooth	6–8	single anterior to 1st gill	21–40 × 11–16.1.1.1.11–16
nilsodhneri	smooth	6	single ventral to 1st gill	25 × 24–30.1.1.1.24–30
plebeia	smooth	4–8	single ventral to 1st gill	20–38 × 32–69.1.1.1.32–69
striata	smooth	4–6	single between 1st and 2nd gills	42 × 26.1.1.1.26
wellsi	with singular triangular appendage	6	single ventral to 2nd gill	20–21 × 10–11.1.1.1.0–11

T. hamnerorum, like the majority of species of *Tritonia,* has an elongate stalk leading to the receptaculum seminis. The receptaculum, in a few species, *T. manicata* Deshayes, 1839, *T. lineata* Alder and Hancock, 1848 (Schmekel and Portmann, 1982) and *T. nilsodnheri* Marcus, 1983 (present study), is sessile or has a very short stalk.

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Table 1. Continued

Inner lateral	2nd lateral	Penis	References
single denticle	smooth	conical	Odhner, 1926; Marcus, 1983; present study
up to 15 denticles	4–5 denticles	conical	Marcus and Marcus, 1967
smooth	smooth	conical	Odhner, 1926; Marcus, 1983; present study
denticulate	smooth	conical with apical annulation	Bouchet, 1977
smooth	smooth	recurved at apex	Marcus, 1983
smooth	smooth	recurved at apex	Odhner, 1939
with 5–7 denticles	smooth	short, rounded	Present study
denticulate in juveniles, smooth in adults	denticulate in juveniles, smooth in adults	short to elongate rounded or conical	Thompson and Brown, 1984
smooth	smooth	short conical	Haefelfinger, 1963
smooth or with one denticle	smooth	flagelliform	Tardy, 1963; present study
denticulate in juveniles, smooth in adults	smooth	—	Thompson and Brown, 1984
smooth	smooth	elongate flagelliform	Haefelfinger, 1963
denticulate	denticulate or smooth	flagelliform	Marcus and Marcus, 1967

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