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SHORT COMMUNICATION

Molluscan diversity in shallow water hydrothermal vents off Kueishan Island, Taiwan

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Abstract Hydrothermal vents are among the most 'extreme' habitats in the marine ecosystem, with increased water temperature, drastically different pH to the surrounding water, and richness in toxic substances such as hydrogen sulphide and methane. Although perhaps better recognised as deep-sea habitat, vents actually occur in shallow water within SCUBA diving range in various parts of the world. Kueishan Island, Taiwan is one location where these shallow vents occur, and with a pH as low as 1.52 it is one of the most 'extreme'. Although the faunal composition of shallow Kueishan vents have been previously reported, some molluscan species, however, were misidentified. Here we present a corrected and updated list of molluscs inhabiting hydrothermally influenced areas off Kueishan Island, a total of 13 species including six new records. Documentation of biodiversity is key in understanding ecosystem functioning, and we briefly discuss the potential significance of the apparent abundance of carnivorous and suspension feeding molluscs in Kueishan vents.

Keywords Hydrothermal vent · Chemosynthetic ecosystems · Mollusca · Gastropoda · Polyplacophora

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Introduction

Hydrothermal vents are home to 'extreme' ecosystems heavily nourished by chemosynthetic primary production based on reduced compounds contained in emerging geofluids (Van Dover 2000). Vents occur in both deep-sea and shallow water, and although biomass is often high due to an increased energetic input, the species richness is usually low as few species can tolerate the toxic and highly acidic/basic environment (Grassle, 1989). In deep-sea hydrothermal vents, many endemic species occur, of which the most abundant ones tend to have evolved symbiotic relationships with chemosynthetic microbes. This is not the case in shallow-water hydrothermal vents, which rarely host endemic species; instead, the species present are usually a subset of species present in the general area that are capable of tolerating the 'extreme' environment (Thiermann et al. 1997; Melwani and Kim 2008). The main difference between deep and shallow vents is the proportion of energy provided by photosynthesis vs chemosynthesis, with photosynthesis being an important source of primary production in shallow vents but much less so in deep vents (Tang et al. 2013).

Molluscs are a major component of hydrothermal vent ecosystems, both deep and shallow, and occupy a wide range of ecological niches (Sasaki et al. 2010). The shallow vent site off Kueishan Island (also known as Gueishan Island, Turtle Island, or Kueishantao) is no exception, with a large proportion of megafauna found being molluscs (Chan et al. 2016: Fig. 7). A small island about 11 km off Yilan County, Taiwan, Kueishan Island is home to a number of vapour-rich vents in both shallow (10–30 m deep) and moderately deep (200–

300 m) waters (Bouchet and von Cosel 2004; Jeng et al. 2004; Wang et al. 2014; Chan et al. 2016). The shallow vents (over 30 in an area of 0.5 km^2; Chen et al. 2005a) which exude hydrogen sulphide (Tang et al. 2013) are especially significant as its fluids are extremely acidic with pH as low as 1.52 (Chen et al. 2005b) and represent one of the most perilous environments for life. Although the common molluscs present there were reported by Chan et al. (2016), taxonomic identifications of some molluscan species were incorrect. Here, a revised and updated list of molluscan species inhabiting the hydrothermally influenced area is provided based on the same material supplemented by specimens from further collecting events, and the significance of the apparent skew in ecological niches they occupy is discussed in the light of ecosystem functioning.

Materials and methods

Molluscan species were collected via SCUBA diving conducted from July 2014 to June 2015, totalling 20 dives. The depth range was small, between 13 to 15 m deep (Table 1). Both intense venting regions and vent periphery (150 m – 300 m from the central vent region) were sampled, but molluscs were mostly from the periphery zone, starting to occur at distances of 150 m from the vents (sensu Chan et al. 2016). Specimens collected were fixed and stored in 99% ethanol and identified morphologically aided by a dissecting stereomicroscope (SZX9, OLYMPUS, Tokyo). Furthermore, scanning electron microscopy (SEM) was carried out for polyplacophoran (chiton) valves, girdle, and radula as well as gastropod radulae. These elements were dissected from specimens fixed and preserved in 99% ethanol, and prepared by soaking in half-strength household bleach to remove tissue followed by thorough rinsing in Milli-Q water. A table-top SEM (TM-3000, HITACHI, Tokyo) in Japan Agency for Marine-Earth Science and Technology (JAMSTEC) was used for observation at 15 kV after the specimens were dried and mounted on carbon tape.

Results and discussion

A total of 13 molluscan species were identified from the Kueishan vent material (Table 1; Fig. 1), including 12 gastropods and a single chiton. As only seven species were previously reported, this represent almost a doubling in molluscan species richness. None of the molluscs inhabited areas around the vent mouth; instead, they inhabited the vent peripheral zone (start from 150 m apart from vents) which is still highly influenced by the vent (Chan et al. 2016). Also shown in Table 1 is the identity reported in Chan et al. 2016. Following Chan et al. 2016, we regarded 300 m away from the vent orifice as the end of the vent periphery community, after which virtually all species observed within the vent area become replaced by other species. A multivariate nMDS plot (Chan et al. 2016: Fig. 8) clearly showed that the community composition clustered with non-vent influenced control sites instead of vent or vent periphery sites. The area within 300 m of the vent orifice is known to have a generally lower pH and dissolved oxygen concentrations compared to those further away; and the concentration of arsenic has been reported to be significantly higher near vent orifices (for details see Chan et al. 2016: Figs. 3–4).

Out of the seven mollusc species previously reported from Kueishan vents, three were misidentified for various reasons, resolved as follows. The chiton species was the most problematic due to the corrosion of valves and girdle scales. However, SEM investigation revealed smooth insertion plates, slit-formula of 12/1/12, lack of jugal lamina, and sizes of girdle scales matching *Ischnochiton* (Schwabe 2010; J. Sigwart pers. comm.). Radula characteristics, girdle scales, and valve sculpture further placed it in the *I. comptus* complex (Owada 2016), and quincuicial granulations in the central area of valves enabled identification of the Kueishan specimens as *I. comptus* (Owada 2016; B. Sirenko pers. comm.). The second difficult case was the vermetid worm shell. The same species was listed by Chan et al. (2016) as *Dendropoma dragonella* (Okutani & Habe, 1975), who noted the "presence of opercular valves distinguished *Dendropoma* from the morphologically similar genus *Serpulorbis*" (Fig. 7 caption). However, re-examination of the specimens by the junior author revealed a lack of operculum; close examination of the original photographs suggested that the 'operculum' reported earlier was actually the foot which enclosed the aperture (see Fig. 2b). The surface sculpture, coiling tendency, as well as the characteristic purplish colouration (Hasegawa 2017) then allowed its determination as *Thylacodes nodosorugosus* (Lischke, 1869). Note that *Serpulorbis* is a junior objective synonym of *Thylacodes* (Golding et al. 2014). A third misidentified species was the calyptraeid slipper-limpet *Bostrycapulus gravispinosus* (as *B. aculeatus*), this was largely due to the fact that all spiny slipper-limpets were once considered to be a single global species *B. aculeatus* (Collin 2005; Collin et al. 2010). The name *B. gravispinosus* is currently used for western Pacific populations, including Taiwan (listed as *Credipula* (*Bostrycapulus*) *gravispinosus* in Okutani 2017).

The most abundant species that occurred close to vent orifices was the slipper limpet *B. gravispinosus*, which was found in closely-packed assemblages on hard substrates (Fig. 2a), together with the worm shell *T. nodosorugosus* which was also common (see Chan et al. 2016: Fig. 7C). The dove shell *A. miser* was relatively common in the periphery zone close to the vent effluent; only at some distance away do the muricid *Ergalatax contracta* (Reeve, 1846) and the chiton *I. comptus* appear. For detailed information on the relative abundance of each species please see Table 1.

Table 1 List of molluscan species found in shallow hydrothermal vent sites off Kueishan Island, Taiwan and their relative abundance (abundant > common > uncommon). Identity reported earlier by Chan et al. (2016) is also listed for reference, the spellings are as they were on the first appearance on the published paper including misspelt scientific names. Sampling localities and their approximate distance from vent orifices is also shown

Class	Family	Species	ID in Chan et al., 2016 [sic.]	Abundance Scale	Region	Depth	Longitude, Latitude
Polyplacophora	Ischnochitonidae	*Ischnochiton comptus* (Gould, 1859)	*Chiton komaiana* Is. & Iw. Taki, 1929	Common	Peripheral region	14 m	24.50.058 N, 121.57.779E
Gastropoda	Calyptraeidae	*Bostrycapulus gravispinosus* (Kuroda & Habe, 1950)	*Bostrycapulus aculeatus* (Gmelin, 1791)	Abundant	Peripheral region	13 m	24.50.054 N, 121.57.723E; 24.50.027 N, 121.57.725E
	Vermetidae	*Thylacodes nodosorugosus* (Lischke, 1869)	*Dendropoma dragonella* (Okutani & Habe, 1975)	Abundant	Peripheral region	13 m	24.50.027 N, 121.57.725E
	Cypraeidae	*Monetaria moneta* (Linnaeus, 1758)	*Cypreae* Linnaeus 1758 spp.	Uncommon	Peripheral region	14 m	24.50.058 N, 121.57.779E
	Mitridae	*Strigatella scutulata* (Gmelin, 1791)	Not listed	Uncommon	Peripheral region	13 m	24.50.027 N, 121.57.725E
	Muricidae	*Ergalatax contracta* (Reeve, 1846)	*Ergalatax contrata* (Reeve, 1846)	Uncommon	Peripheral region & 300 m away from vent	13–15 m	24.50.027 N, 121.57.725E; 24.50.058 N, 121.57.779E; 24.50.088 N, 121.57.576E
	Ranellidae	*Monoplex nicobaricus* (Röding, 1798)	*Monoplex nicobaricus* (Röding, 1798)	Uncommon	Peripheral region & 300 m away from vent	13–15 m	24.50.027 N, 121.57.725E; 24.50.088 N, 121.57.576E
		Monoplex vespaceus (Lamarck, 1822)	Not listed	Uncommon	300 m away from vent	15 m	24.50.088 N, 121.57.576E
	Columbellidae	*Anachis miser* (Sowerby I, 1844)	*Anachis misera* (Sowerby, 1844)	Common	Peripheral region	13–14 m	24.50.027 N, 121.57.725E; 24.50.058 N, 121.57.779E
		Pardalinops testudinaria (Link, 1807)	Not listed	Uncommon	Peripheral region	13 m	24.50.027 N, 121.57.725E
		Pyrene punctata (Bruguière, 1789)	Not listed	Uncommon	300 m away from vent	15 m	24.50.088 N, 121.57.576E
	Buccinidae	*Pollia mollis* (Gould, 1860)	Not listed	Uncommon	Peripheral region	13 m	24.50.027 N, 121.57.725E
	Conidae	*Conus muriculatus* Sowerby I, 1833	Not listed	Uncommon	300 m away from vent	15 m	24.50.088 N, 121.57.576E

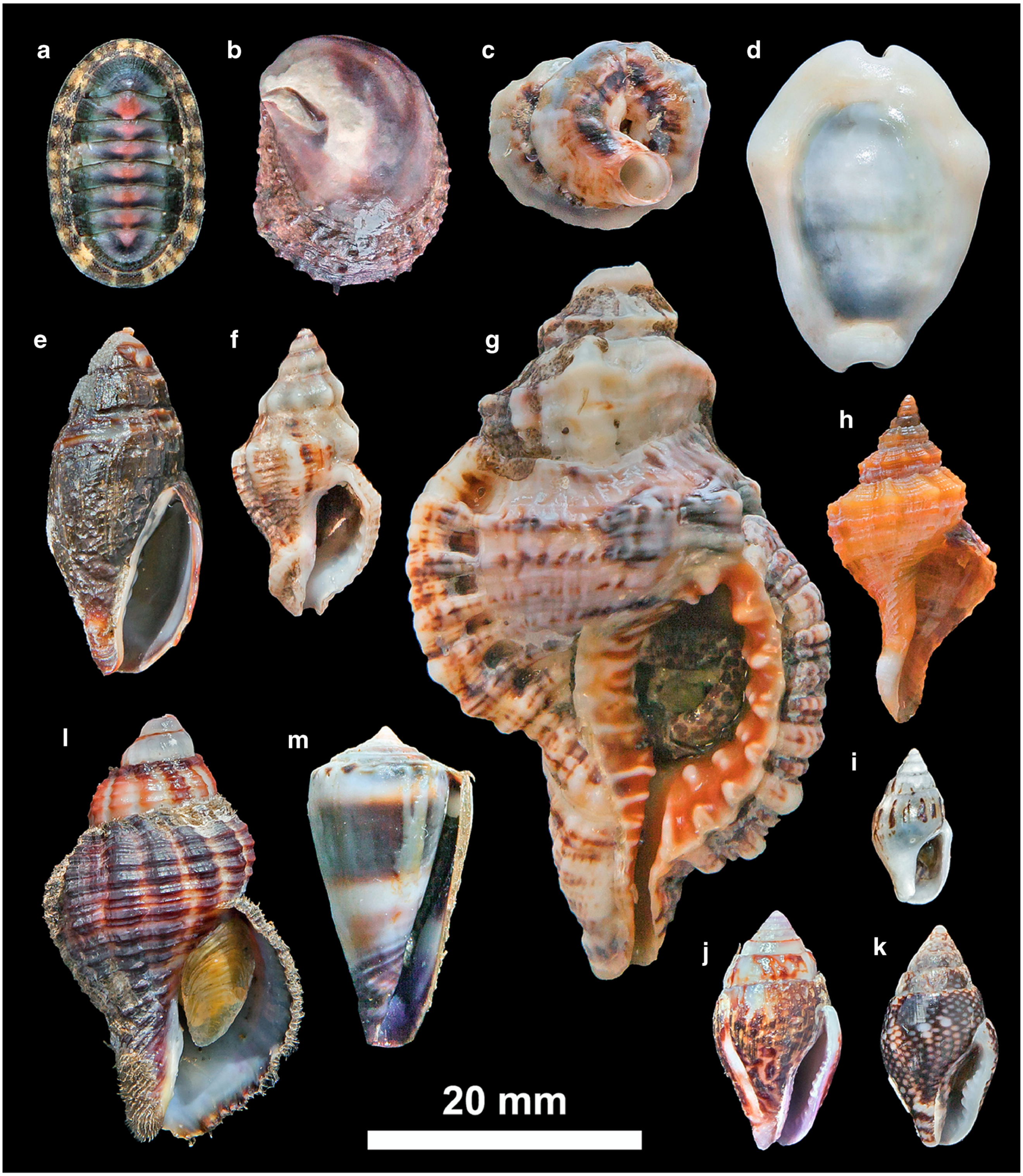

Fig. 1 Representative specimens of the 13 mollusc species collected from shallow hydrothermal vents off Kueishan Island, Taiwan. **a**: *Ischnochiton comptus*; **b**: *Bostrycapulus gravispinosus*; **c**: *Thylacodes nodosorugosus*; **d**: *Monetaria moneta*; **e**: *Strigatella scutulata*; **f**: *Ergalatax contracta*; **g**: *Monoplex nicobaricus*; **h**: *Monoplex vespaceus*; **i**: *Anachis miser*; **j**: *Pyrene punctata*; **k**: *Pardalinops testudinaria*; **l**: *Pollia mollis*; **m**: *Conus muriculatus* Sowerby I, 1833

No bivalve molluscs were found to inhabit the vent periphery throughout the intensive dive surveys. Two bivalve species, *Ostrea denselamellosa* Lischke, 1869 and *Lopha cristagalli* (Linnaeus, 1758) were reported by Chan et al. (2016). We here note that although the identification of *O. denselamellosa* was accurate, '*L. cristagalli*' should be

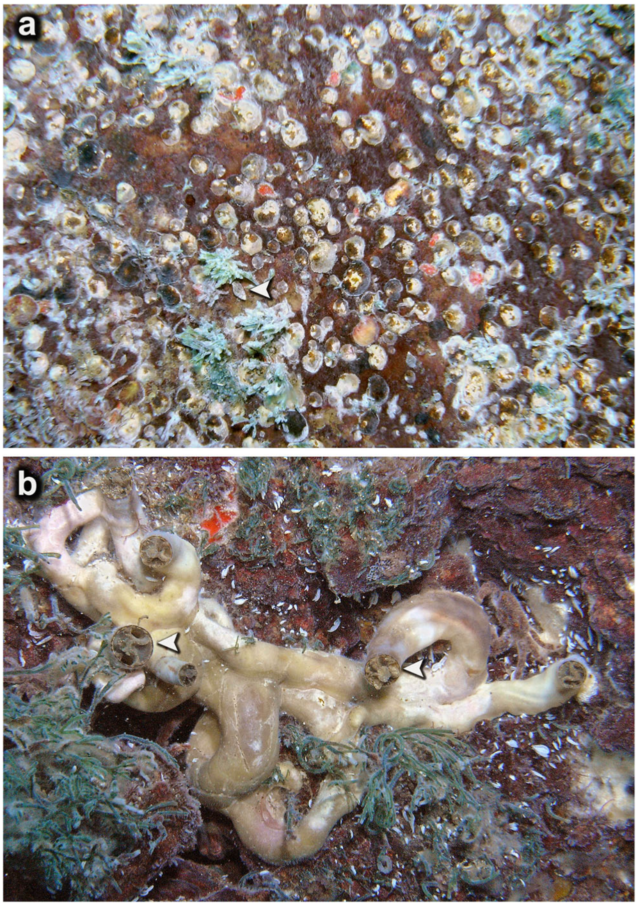

Fig. 2 In situ photographs at the periphery zone of Kueishan shallow water hydrothermal vents. **a**: Dense aggregations of the slipper limpet *Bostrycapulus gravispinosus*, arrowhead indicate a specimen of the dove shell *Anachis miser*. **b**: Close-up of a small aggregation of the worm shell *Thylacodes nodosorugosus*, note the lack of operculum as shown by individuals indicated by arrowheads

identified as *Hyotissa hyotis* (Linnaeus, 1758). Both bivalves were rather large, reaching over 150 mm in shell length. These are not considered here as being part of the core Kueishan vent community as they were only found over 300 m away from the vent mouth and were common in regions >1000 m away from vents. However, it is important to note that both are filter-feeders and may benefit from the vent plume in a similar way as the gastropods closer to vent orifices, which needs testing in future studies with stable isotopes. Furthermore, at over 700 m away from the vent mouth we observed the occurrence of fasciolariid spindle snail *Pleuroploca trapezium* (Linnaeus, 1758), tegulid top shell *Tectus pyramis* (Born, 1778), ovulid *Diminovula alabaster* (Reeve, 1865), pearl oyster *Pinctada margaritifera* (Linnaeus, 1758), as well as some jewel box clams *Chama* sp. and arc clams *Arca* sp. The occurrence of *D. alabaster* is linked to the higher presence of corals at this distance from the vents (Chan et al. 2016). It has been shown that coral growth is greatly inhibited by acidic water (Chan et al. 2012) and the blocking of sunlight for photosynthesis around Kueishan vents (Chan et al. 2016), and the presence of high coral cover indicate that the effect of vent effluents has been greatly reduced at this point. For this reason, we do not include these molluscs as part of the Kueishan vent fauna.

Only one strictly grazing molluscan species, the chiton *Ischnochiton comptus*, was found near the vents. Such low diversity of grazers is unusual for molluscan communities at shallow depths with algae being present (Chan et al. 2016). Given the combination of chemosynthesis and photosynthesis at the Kueishan site, *I. comptus* most likely ingest both algae and bacterial mat. Although cowries have mixed diets depending on the species, *Monetaria moneta* (relatively uncommon on the vent peripheral region when compared to the chiton) has been observed to primarily graze on algae (Renaud 1976) and may therefore exhibit a similar lifestyle to the chiton at Kueishan vents. Dove shells (Columbellidae) are also uncommon at the vent peripheral region and have extremely variable feeding ecology among different species and may feed on animals, carrion, algae and other plant matter; they may even be capable of filter-feeding (Hatfield 1979; Taylor et al. 1980; Taylor 1987). As one species appear to have multiple food sources (Hatfield 1979), the exact energy source of columbellid gastropods at the Kueishan vents cannot be determined at this stage (although they are likely omnivores). Most gastropod species were either carnivorous / scavenging (including muricids, buccinids, ranellids) or suspension feeders (the vermetid worm shell *Thylacodes nodosorugosus* and the slipper-limpet *Bostrycapulus gravispinosus*). This, and the fact that very few algae grazers were present, is likely linked to influences of the acidic and poisonous vent plume on the immediate environment. The vent plume from the shallow Kueishan vents rises right to the surface, killing off plankton and larger organisms (including fishes), which then fall to the vent sites underneath (Chan et al. 2016). This falling organic matter is likely the major energetic source for the molluscs inhabiting the vent periphery, and explains why there is a much higher abundance of suspension feeders and scavenging carnivores compared to grazers.

Molluscan species living in the shallow water vent environment in Castello d'Aragonese often suffer from acidic corrosion of shell, resulting in the removal of periostracum or having pitted shells (Hall-Spencer et al. 2008). Many molluscan species inhabiting the shallow water vents in Kueishan Island were found to have a similar surface corrosion. The chiton *I. comptus* exhibits surface corrosion of the valves and girdle scales, and for gastropods corrosion was most evident in the triton *M. nicobaricus*, the mitrid *S. scutulata,* the slipper limpet *B. gravispinosus*, and the dove shell *A. miser*; although all species found in the periphery zone showed at least some corrosion (Fig. 1). Even at 300 m away from vent, the conid *C. muriculatus* was found to have most of its periostracum dissolved and shell surface corroded, indicating that the influence of acidic vent fluid extended at least 300 m away from the vent orifices. Chen et al. (2015) revealed that populations of the dove shell *Anachis* living in regions with lower pH have different protein expression than the populations living in higher pH sites. This suggests the lowered pH of the vent environment in Kueishan Island can affect the physiology and shell growth of gastropods.

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