DOI: http://doi.org/10.18941/venus.75.1-4_93

Possible Mimicry in the Galeommatid Bivalve *Scintilla philippinensis* (Bivalvia: Galeommatidae) to Nudibranchs and Crabs

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Mimicry has been widely observed in many aquatic animals including fishes and invertebrates in relation to predation, anti-predation, warning or reproduction (Gould, 1980; Randall, 2005). Among mollusks, it is well documented in gastropods, bivalves and cephalopods (Norman *et al*., 2001; Roe *et al*., 2001; Hanlon *et al*., 2008; Krajewski *et al*., 2009; Huffard *et al*., 2010; Okamoto *et al*., 2017). Many ovulid gastropods (egg cowries) show background-matching mimicry for octocorals on which they live and feed (Sánchez *et al*., 2006). The freshwater mussels *Lampsilis* spp. mimic fish, insects and invertebrates with specialized mantles to lure host fish to attach their parasitic glochidia (Haag *et al*., 1995; Haag & Warren, 1999; Zanatta & Murphy, 2006). Recently much attention has been paid by marine and evolutionary biologists to mimic octopuses (Norman *et al*., 2001; Roe *et al*., 2001; Hanlon, 2007; Krajewski *et al*., 2009; Hanlon *et al*., 2010; Huffard *et al*., 2010; Coker, 2013; Saraswati *et al*., 2014). However, it is not evident that mimic octopuses are a case of Batesian mimicry, mimicking poisonous flatfish (Hanlon *et al*., 2008).

During our marine faunal survey in Palawan Island, the Philippines, we found living individuals of the galeommatoidean bivalve *Scintilla philippinensis* Deshayes, 1856. This species is free-living, not commensal unlike many other species in the superfamily. It lives under coral blocks or boulders, and has a rather wide distribution in the tropical and subtropical areas of the Indo-West Pacific including the Philippines, Okinawa and Phuket (Lützen & Nielsen, 2005; Kubo, 2012; Huber, 2015). According to Kurozumi *et al*. (2007), the Japanese population might be a separate species judging by differences in the color of the mantle and shell. Galeommatoideans are unique among bivalves in having a well-developed foot with modified dorso-ventrally flattened sole for crawling and specialized papillae or tentacles on the mantle edge, as well as their commensal habitat in many species (Ponder, 1998; Goto *et al*., 2012). Species of the genus *Scintilla* have specialized mantle tentacles and show unique creeping, climbing and jumping behaviors (Savazzi, 2001; Lützen & Nielsen, 2005). It has been reported that they mimic nudibranchs (Onuki & Hayase, 2016) and crabs (Awase Tideland Natural Environment Investigation Committee, 2005; Kurozumi *et al*., 2007). Two additional forms of mimicry were displayed by the same individuals of *S. philippinensis* and are reported herein.

Materials and Methods

Two living specimens of *Scintilla philippinensis* (shell length/height: 14.1/9.6 mm, 15.0/9.6 mm) were collected from the lower side of a dead coral rock (*ca*. 30 cm in size) in shallow water off El Nido, Palawan Island, the Philippines (11˚04´41˝N, 119˚24´45˝E), on September 15, 2016. These were kept in a small plastic container (1.3 L) for four days at a room temperature. Water was changed daily. Their mimic behaviors were recorded by digital cameras (COOLPIX AW130, Nikon Co., Ltd., Tokyo; IXY 930IS, Canon Co., Ltd., Tokyo), using video mode. Some still photos were taken at night with an LED light.

Results and Discussion

Scintilla philippinensis possibly showed resemblance to two kinds of benthic animals: nudibranchs and crabs. The nudibranch form (Fig. 1A, B) was characterized by slightly opening the shells and standing up with the ventral side of the shells perpendicular to the bottom. The animal bore a pair of lateral processes originating from the posterior edge of the mantle, which looked like the paired rhinophores of a nudibranch, and antero-dorsal and lateral processes that resemble its gills. In addition, the anterior processes (gills) extended further than the posterior ones (rhinophores). The terminal tips of the posterolateral processes were more markedly tinged with darker purple than those of the antero-lateral and dorsal processes (arrowed in Fig. 1A). The long, slender foot resembled the tail of a nudibranch. The mantle entirely covered the shells except for a dorsal patch on each shell. This form was not as active as the crab form (see below), but slightly swung the foot.

In contrast to the nudibranch form, the crab form (Fig. 2A, B) obliquely placed the dorsal side of the right shell in contact with the bottom. The central mantle processes were curved dorsally, the lateral ones ventrally or dorsally. The shell was almost entirely covered with the mantle and the curved processes, possibly corresponding respectively to the carapace and walking legs of a model crab. The dorsal processes were sometimes directed ventrally to mimic the pincers of the model (arrowed in Fig. 2A). This form was highly active, with a powerful jet of water from the posterior opening of the mantle. In this case the foot was fully expanded anteriorly (1.0–1.5 s in Fig. 3) and then swung posteriorly during the anterior movement (2.0 s). Finally, the foot seemed to be utilized as a brake (Figs 2B, 3). During one jetting, it moved a distance of *ca*. 40 mm, 2.5–3 times as long as the shell.

Both forms exhibited a resting mode with contraction of the mantle processes. These were observed after showing the mimic behaviors. In the nudibranch form (Fig. 4A, B), the ventral side of the shells was in contact with the bottom, while in the crab form (Fig. 5A–C), it was the dorsal side.

Small fecal pellets were seen on the bottom of the container during the days of observation, indicating that feeding and excretion occurred in the container.

It seems that one form of *S. philippinensis* mimics certain nudibranchs. It is difficult to specify their model animals exactly, but considering the presence of the structures similar to oral tentacles, rhinophores and anal gills of nudibranchs, the model candidates may be Euctenidacea (= Anthobranchia sensu Wägele & Willan (2000)). Some species of

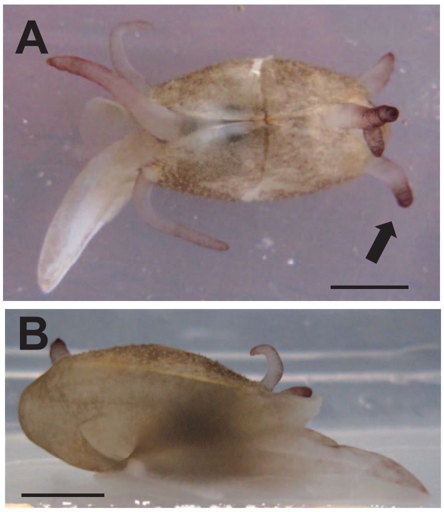

Fig. 1. Possible mimicry in *Scintilla philippinensis*, nudibranch form. **A**. Dorsal view, posterior process arrowed. **B**. Ventrolateral view. Scales = 5 mm.

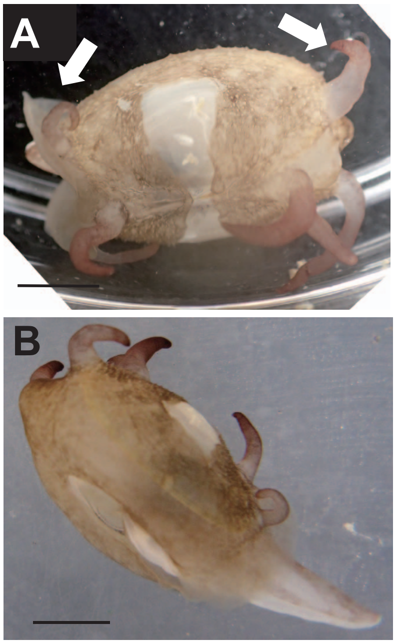

Fig. 2. Possible mimicry in *Scintilla philippinensis*, crab form. **A**. Dorsolateral view, claiming wall of container, cheliped-like process arrowed. **B**. Ventrolateral view. Scales = 5 mm.

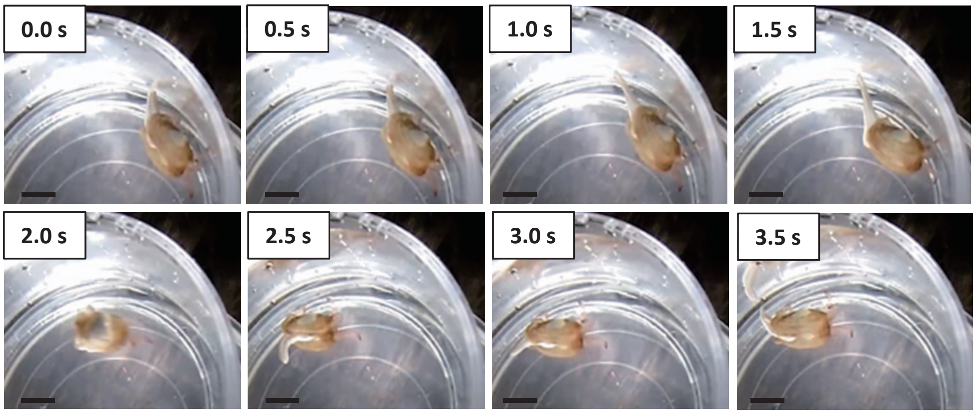

Fig. 3. Sequential jumping movement of crab form of *Scintilla philippinensis*. Number indicates time (second) after starting. Scales = 10 mm.

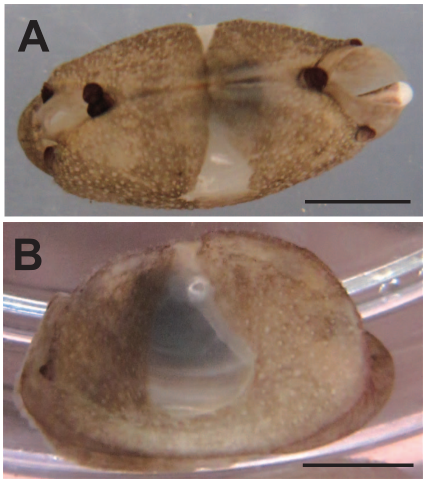

Fig. 4. Resting mode of nudibranch form of *Scintilla philippinensis*. **A**. Dorsal view. **B**. Dorsolateral view. Scales = 5 mm.

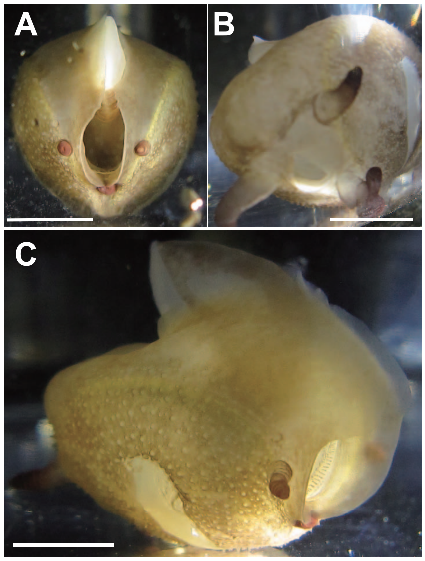

Fig. 5. Resting mode of crab form of *Scintilla philippinensis*. **A**. Anterior view. **B**. Posterior view. **C**. Anterolateral view. Scales = 5 mm.

this nudibranch group are known to have strong defense mechanisms based on accumulation of defensive metabolites recovered from their prey sponges (Faulkner & Ghiselin, 1983). Accordingly, many marine organisms are considered to mimic these nudibranchs, especially during their juvenile stages, such as fishes (Randall, 2005), holothurians (Gosliner & Behrens, 1990), amphipod crustaceans (Goddard, 1984), velutinid gastropods (Gosliner *et al*., 1996), and polyclads (Perrone & Doneddu, 2001). Many eucteidaean nudibranchs are distributed in the tropical waters of Southeastern Asia, and over 140 species of the group were known from the South China Sea (Sachidhanandam *et al*., 2000), one or more of which may turn out to be the models for this bivalve mimicry.

The crab form may mimic a xanthid crab, some of which are toxic and distributed in the Philippines (Asakawa *et al*., 2015), judging by the general shape and coloration of the carapace-like shells covered by the mantle in addition to the crabwalk-like movements. In particular, the cheliped-like processes of the mantle are terminally tinged with dense colors, which are similar to the colors of the dactylus and palm of some xanthid crabs (see Figs 2 & 3 in Saito *et al*., 2006). In the toxic xanthid crab *Atergatis floridus*, that is distributed also in the Philippines (Asakawa *et al*., 2015), these parts are highly toxic in comparison with the basal segments of the cheliped (Saito *et al*., 2006). The conspicuousness of the toxin-bearing parts seems to be effective as a warning for visual predators, which may be mimicked by *S. philippinensis*. Thus, both nudibranch and crab forms may be regarded as examples of Batesian mimicry if the model animals can be specified more accurately (cf. Joron & Mallet, 1998).

The bivalve might maintain suspension-feeding during the resting mode, because both anterior and posterior openings of the fused mantle were expanded (see Figs 4A, B, 5A–C).

The problem that needs to be resolved is to identify the kinds of advantages the possible mimicry confers. Although more precise experiments and field observations are necessary to test the mimic hypothesis, the following scenario may be possible. The mimicry can be efficient against visual predators such as fish (Krajewski *et al*., 2009), especially when the bivalve is exposed to them by certain disturbances such as waves. The bivalve may even adopt two tactics for the same predator. The first form may resemble a nudibranch with chemical defenses, and then the second form may be similar to a crab with high escape activity and mechanical (and supposedly chemical) defense. The rapidly escaping crab form may startle attacking visual predators.

Much attention has been paid to the remarkably diverse life styles of the superfamily Galeommatoidea by marine and evolutionary biologists, and especially to symbiosis with other marine invertebrates (Bieler & Mikkelsen, 1992; Savazzi, 2001; Anker *et al*., 2005; Goto *et al*., 2011, 2012; Li *et al*., 2012). The specificity and relationships with the symbiotic hosts have been relatively well documented. Species of the genus *Scintilla* are characterized by the simple shell and their free-living habits, but the group has been shown to be polyphyletic based on a molecular analysis (Goto *et al*., 2012). Epibenthic habits and a muscular foot for snail-like locomotion are common in free-living galeommatoideans (Bieler & Mikkelsen, 1992; Goto *et al*., 2012), but few studies are available of the behavior and ecology of the free-living species and especially the possibility of mimicry. Other types of mimic behavior could be found in these bivalves, because the morphology of the mantle, foot and tentacles is highly variable in the free-living taxa (Bieler & Mikkelsen, 1992). In *S. philippinensis*, their sympatric model animals may be also specific, although mimicry is imperfect (cf. Huffard *et al*., 2010). Further the following questions should be clarified in the future:

(1) how does the bivalve detect predators?
(2) how is switching between nudibranch and crab forms regulated?

In summary, living specimens of the galeommatoid bivalve *S. philippinensis* collected from Palawan Island, the Philippines, likely mimic nudibranchs and crabs with the mantle, mantle processes and foot. It is based on general appearance in the former form and by the imperfect shape and quick locomotion in the latter. Although symbiosis is conspicuous in the superfamily Galeommatoidea, mimicry is not sufficiently investigated as yet.

Supplemental Material

Supplemental video of the mimicking behavior of *Scintella philipinensis* in a plastic container is available at http://www.momo-p.com/index.php?movieid=momo171114sp01b

Acknowledgments: We would like to express our sincere thanks to Prof. Jun Nishikawa for his encouragements, and to Mr. Hirofumi Kubo for his identification of *Scintella philipinensis*. This study was partially supported by grants-in-aid from the Japan Society for the Promotion of Science (Kaken No. 26304030; the Asian Core-to-Core program).

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(Accepted July 13, 2017)

ベッコウマメアゲマキの擬態の可能性について

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要　約

ウロコガイ科二枚貝ベッコウマメアゲマキ *Scintilla philippinensis* Deshayes, 1856 の生体がフィリピン・パラワン島で採集されたが，外套膜とその膜上の突起，足を用いてウミウシ類及びカニ類に擬態と考えられる行動が観察された。ウミウシ類型の場合，外套膜を変形させて形態を似せる。カニ類型の場合には形態的類似性だけでなく足も用いて行動も真似る。ウロコガイ上科は他の動物に共生することで知られるが，擬態に関する知見は少ないので，今後のより詳細な研究が待たれる。