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Macrosymbiotic association of the myid bivalve *Cryptomya* with thalassinidean shrimps: Examples from modern and Pleistocene tidal flats of Japan

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Abstract

Macrosymbiosis, a macroscopic-scale interspecific association, between the myid bivalve *Cryptomya* and thalassinidean shrimps is described. In modern tidal flats, living individuals of *Cryptomya truncata* are observed to protrude their posterior ends into the burrow lumen of thalassinidean shrimps such as *Nihonotrypaea japonica* and *Upogebia yokoyai*. Furthermore, a fossil impression of *Cryptomya busoensis* occurring in a Pleistocene tidal flat deposit of the Shimosa Group, similarly has attached its posterior end to a fossil upogebiid burrow, *Psilonichnus* isp. Both *Cryptomya* species, which are characterized by extremely short siphons, probably utilize the sediment/water interface on the internal surface of the burrow. As the fossil record of *Cryptomya* dates back to the Miocene and such a mode of occurrence can be recognized even in the rock record, careful observation would be expected to reveal the origin and evolution of the characteristic macrosymbiosis.

Keywords: Macrosymbiosis; *Cryptomya*; Thalassinidean shrimps; Recent; Pleistocene; Japan

1. Introduction

Symbiosis was originally defined as a strict association of individuals belonging to two or more species, regardless of whether or not they are mutually advantageous (Bary, 1879 in Savazzi, 2001). Among Bivalvia, two categories of symbiosis can be recognized, namely, microsymbiosis and macrosymbiosis (Savazzi, 2001). The former is referred to the case where microscopic endosymbionts live within a host bivalve (Savazzi, 2001). Most of the studies on symbiosis in bivalves can be classified in this category, because photosymbiosis and chemosymbiosis, of which endosymbionts are microscopic zooxanthella or bacteria that oxidize sulphides or methane, have received much attention (e.g., Majima, 1999; Savazzi, 2001; Pervesler and Zuschin, 2004; and references therein). On the other hand, macrosymbiosys is a symbiotic association that can be recognized at a macroscopic scale (Savazzi, 2001). Although macrosymbiosis is easily recognized in fossil records if the associated organisms are preserved *in situ*, this has received less attention (Savazzi, 2001).

Savazzi (2001) made a comprehensive review of bivalves' macrosymbioses, and stressed such examples as embedment or attachment of bivalves to host animals, and as bivalves that provide habitats for other macrosymbionts. The other style of macrosymbiosis, which likely has high preservation potential in the rock record and therefore is worth considering in palaeoecology, is that mediated by a burrow system of a host animal as seen in the small myid bivalve *Cryptomya*.

Cryptomya is a somewhat compressed bivalve (Keen, 1969), characteristically having extremely short siphons (e.g., Yonge, 1951; MacGinitie and MacGinitie, 1968; Haderlie and Abbott, 1980; Lawry, 1987; Itani and Kato, 2002). Macrosymbiotic association of *Cryptomya* with the other organisms was first

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mentioned by MacGinitie (1934) through his work on the natural history of the burrowing thalassindean shrimps of *Upogebia pugettensis* and *Callianassa californiensis*. He found that *Cryptomya californica* had attached to burrows of the shrimps and inferred a macrosymbiotic relationship for these animals (MacGinitie, 1934; MacGinitie and MacGinitie, 1968). Later, Lawry (1987) observed *Cryptomya californica* occurring in sandy mudflats of Oregon, USA. According to his observations, *Cryptomya californica* burrowed beneath the seafloor, down to 50 cm (Lawry, 1987). Because the bivalve with very short siphons embedded a part of its shells into the tunnels of *C. californiensis*, he confirmed this as a macrosymbiotic association (Lawry, 1987).

Swinbanks (1981) reported a resin burrow cast of *C. californiensis*, which had been attached to by many individuals of *Cryptomya* sp. Although the report was quite instructive of *Cryptomya*'s ecology, it consisted of only one photograph with a brief caption, on a single page of a journal, and details of the interspecific relationships were not described. This contribution thereafter was made more widely known by Bromley (1996, p. 110) with an informative illustration on macrosymbiosis between the clams and shrimps.

The other species of genus *Cryptomya*, i.e., *C. truncata* (=*Venatomya* (*Cryptomya*) *truncata* of Okutani, 2000), which is distributed from central Japan to the East China Sea (Habe, 1977; Okutani, 2000), usually occurs sympatrically with such deep-burrowing thalassinidean shrimps as *Nihonotrypaea japonica* (formerly *Callianassa japonica*; cf., Manning and Tamaki, 1998), *Upogebia major* and *Upogebia yokoyai* (Itani and Kato, 2002). The clams sometimes occur in sediment, a few millimetres aside from the thalassinidean shrimp burrows facing their posterior ends to the burrows (Itani and Kato, 2002). Based on such observations, Itani and Kato (2002) also inferred macrosymbiotic relationships between the shrimps and the clams.

Although macrosymbiosis of *Cryptomya* has attracted attention as noted above, direct evidence that the siphons of the clams were connected to the burrow lumen has not been shown, except for the Swinbanks' (1981) photograph. Also, the detailed structure of the connecting portion has not been described. This is probably because the clams commonly were living in waterlogged, sandy sediments that are too crumbly to allow easy observation.

Recently, Akiyama and Nara (2007) introduced a technique to observe intact three-dimensional sediment fabrics of tidal flats, using a shovel-like apparatus and a peeling technique, and found burrow systems of *U. yokoyai* and *N. japonica*, on which were attached many living individuals of *C. truncata*, from sandy mudflats of southwestern Japan. Although they pointed out the possibility of the macrosymbiotic relationship between the shrimps and the bivalves, detailed description and discussion were not made.

On the other hand, such an association has also been recognized from the rock record. A fossil upogebiid burrow representing *Psilonichnus* isp. (Nara and Kotake, 1997) and an associated fossil impression of *Cryptomya busoensis* were found in Pleistocene tidal flat deposits of the Shimosa Group, which is distributed in the southeastern part of the Kanto district, central Japan (cf., Nara and Kotake, 1997).

The aims of this paper are to describe the associated occurrence of *C. truncata* with the thalassinidean burrows and detailed structures of the point of connection, in the modern tidal flat sediments, along with the Pleistocene examples of *C. busoensis*.

2. Localities studied

Observations were made in modern tidal flats developed in the mouth of the Kamo River of the Ehime Prefecture, southwestern Japan, and in tidal flat deposits of the middle Pleistocene Yabu Formation in the Boso Peninsula, Chiba Prefecture, central Japan. Descriptions of the localities are as follows.

The former observations were made in the mouth of the Kamo River, which runs into the Seto Inland Sea (Fig. 1). Living specimens of *Cryptomya truncata* were found in the sandy mudflats where biogenic mounds formed by the callianassid shrimps, *Nihonotrypaea japonica*, occur commonly.

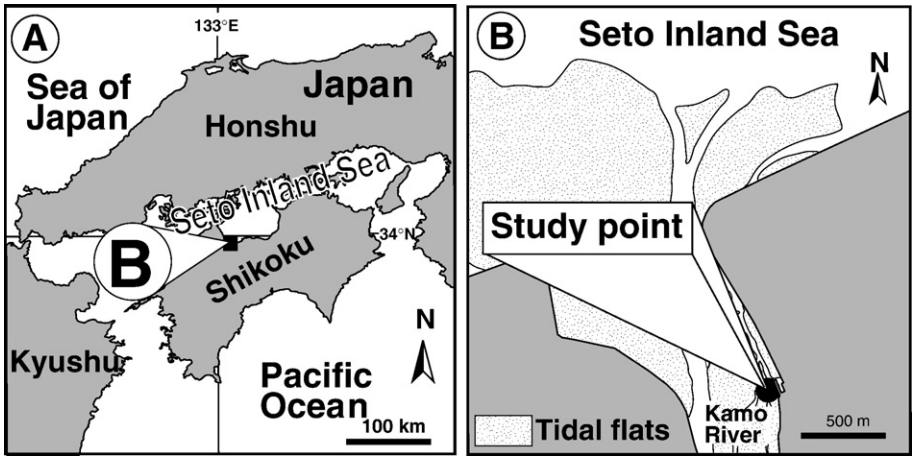

Fig. 1. Locality maps showing the study point and the modern tidal flats developed in the Kamo River.