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## “Shelly softground” colonized by an endobysate bivalve, *Modiolus kurilensis*: an example of taphonomic feedback from the Pleistocene of Kanazawa, Japan

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Received 11 January 1995; Revised manuscript accepted 18 September 1995

**Abstract.** Colonization by an endobysate bivalve *Modiolus kurilensis* was possible only in shelly softground conditions, that is, on a soft bottom with the shells being slightly buried with fine sediment. The Pleistocene Omma Formation, Kanazawa, generally exhibits a shelly bottom carpeted by shells (shell pavement) or a shelly bottom covered by soft sediment too thick to allow colonization by *Modiolus*. The described *Modiolus* colony was found in the lower unit of the Omma Formation, where sealevel change was relatively small and where shelly softground conditions were present. In contrast, *Modiolus* is much less common in the shell beds in the cyclothem middle unit of the formation. An important environmental factor accounting for the uncommon occurrence of *Modiolus* in cycle-bounding shell beds is their repeated physical reworking followed by deposition of soft sediment too thick to be colonized by *Modiolus*.

**Key words:** Shelly softground, taphonomic feedback, bivalve, *Modiolus kurilensis*, *Modiolus modiolus difficilis*, Omma Formation, Pleistocene

### Introduction

This note originated from a find of a well-preserved endobysate bivalve colony underlain by a shell lens in the early Pleistocene Omma Formation. Establishment of the bivalve colony described herein was most probably facilitated by the presence of shell material on an otherwise barren silty sand bottom which was difficult for endobysate bivalves to colonize. In our experience, gregarious colonies of endobysate bivalves are not uncommon, an example being those found in the Pleistocene Jizodo Formation, Boso Peninsula. There is, however, no published taphonomical and paleoecological description of such bivalve colonies. Taphonomically similar examples have been studied by Ziegler *et al.* (1966), Walker and Parker (1976), Johnson (1977) and Wilson (1982), but for much older Paleozoic brachiopod colonies.

Kidwell and Jablonski (1983) proposed a concept of taphonomic feedback for such fossil occurrences, whereby dead hardparts facilitate or inhibit the colonization of a subsequent community. They used the term taphonomic to emphasize the postmortem processes that figure in the availability of dead hardparts, and the term feedback to emphasize that not only does the life assemblage influ-

ence the death assemblage (as in conventional taphonomy), but the death assemblage in turn affects the life assemblages. The concept of taphonomic feedback is distinguished from “ecological succession” in emphasizing that not only living organisms but also dead hardparts influence subsequent life assemblages. Recognition and description of such taphonomic feedback are actually common in earlier studies of modern communities or fossil assemblages. For example, as early as the 1930's, Powell (1937) discussed substratum modification by accumulating shell and its effect on the distribution of marine benthic communities in his study of animal communities in Auckland Harbor in New Zealand. As an ancient example, Aigner (1982) discussed modified substratum conditions as an inferred consequence of high-energy events in Triassic shallow marine deposits of Southwest Germany, and classified them under softground, firmground and hardground.

Kidwell (1989) thoroughly reviewed the literature describing taphonomic feedback from ancient and modern marine environments. Also, she tested taphonomic feedback in thick shell beds in the Miocene of Maryland, by examining relative abundance of shell-gravel dwellers and shell content in the sediments, and concluded that the correlation between them was statistically significant.

This paper describes a simpler, but unambiguous example of taphonomic feedback which acted to establish a colony of an endobryssate bivalve in a shallow-marine environment in the Early Pleistocene of Japan. We also discuss a characteristic substratum condition termed a shelly softground.

### Acknowledgments

We thank R. Majima of Yokohama National University, T. Kamiya and K. Konishi of Kanazawa University for their assistance in the sampling of the large fossil concretion used in this study. A. Kitamura of Shizuoka University kindly gave us useful information related to this study. I. Hayami and T. Kase are also thanked for providing information on living *Modiolus*. Bob Carter of James Cook University and R. Majima improved this manuscript.

### Geologic setting and observation

The bivalve colony was found at the type locality of the Early Pleistocene Omma Formation, along the River Saikawa in a suburb of Kanazawa City, on the Japan Sea coast of central Japan. The Omma Formation is about 200 m thick, and is characterized by at least ten shell-bed bounded sedimentary cycles, which originated from early Pleistocene glacio-eustatic sea-level changes (Kitamura and Kondo, 1990; Kitamura *et al.* 1994). The middle, cyclic part of the Omma Formation comprises alternating shallow (upper sublittoral) and deep (lower sublittoral) molluscan fossil associations. Also, most of the species in the upper sublittoral associations are cold sea type and all the constituents of the lower sublittoral associations are warm sea type, common in the Kuroshio. Such linked changes between water depth and marine climate clearly suggest a glacio-eustatic origin for the cyclic environmental change. In contrast, the lower unit of the formation consists of relatively monotonous bluish-gray, partly brown, fine-grained sandstone with sporadic mollusc and echinoid remains and occasional shell lenses consisting of articulated or disarticulated valves of *Anadara amacula*. The *Modiolus* colony was preserved resting on one of these shell lenses, stratigraphically located 2.5 m above SB3 (fig. 5, Kitamura, 1991a). In the upper transitional unit to the middle unit of the Omma Formation, dense shell beds showing characteristics of stormy condition are present (Kitamura, 1991a). The inferred depositional environment for most of the lower unit is upper sublittoral, within a cold-water oceanographic regime.

A concretionary block sample containing the bivalve colony and of 40×50×20 cm size was extracted, and biostratigraphic observation of shell orientation and disarticulation ratio was made in the laboratory. The block sample is deposited in the Department of Geology, Kochi University.

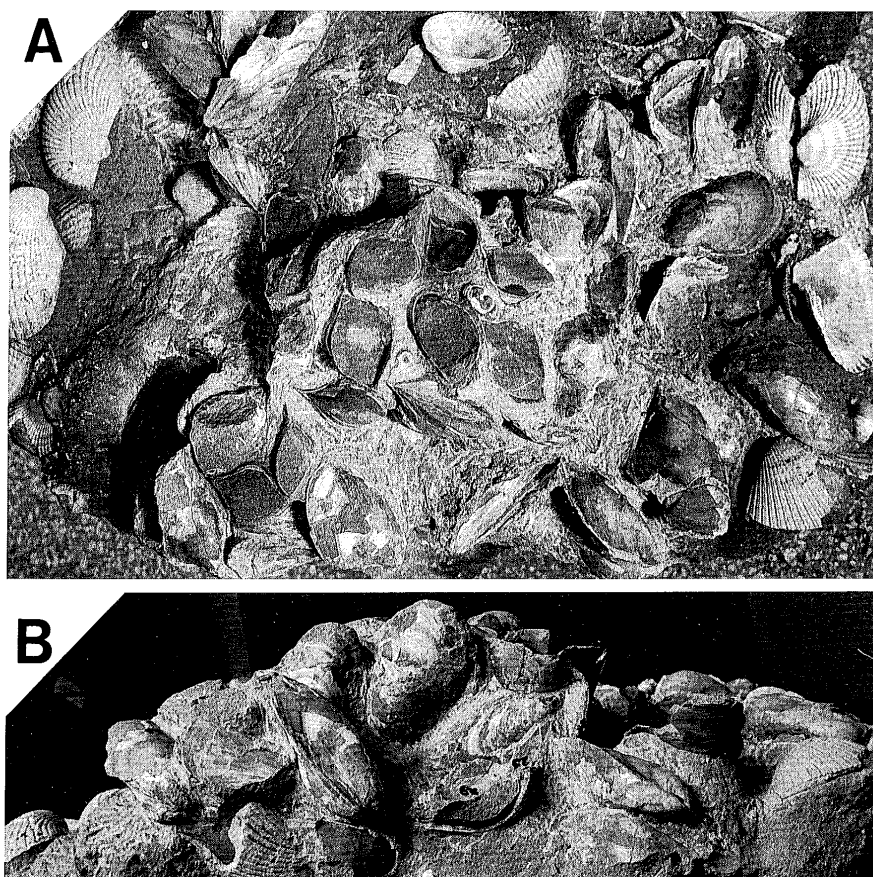
### Description of the colony and the underlying shell lens

Figure 1 shows horizontal and cross-sectional views of the bivalve colony. The bivalve is identified as a living species, *Modiolus kurilensis* Bernard 1983. The well-known synonyms include *Modiolus difficilis* and *Modiolus modiolus difficilis*, and the species is known as "ezohibairigai" in Japanese. Fossils of this species have been reported from the Pleistocene of South Kanto (Oyama, 1973, and many other papers), e.g. the Miyata Formation in the Miura Peninsula and the Jizodo, Yabu and Kiyokawa Formations in the Boso Peninsula, the Pleistocene of Hokuriku including Omma Formation (Kaseno and Matsuura, 1965), and the Pleistocene of Hokkaido (Sakagami *et al.* 1966; Suzuki, 1989). Lenticular concentrations of mostly unabraded shells of *Anadara amacula*, an extinct infaunal arcid bivalve, underlie the *Modiolus* colony. All the shell lenses are only one layer thick. Some of the shells are still articulated, but commonly they gape and are stacked with similar orientation or with opposed postures. No *in-situ* preserved *Anadara* specimen was found in this block (Figure 1), nor in other *Anadara* shell lenses. The shell lenses of *Anadara amacula* in the lower unit of the Omma Formation are, therefore, current- or wave-worked shell concentrations, rather than an *in-situ* occurrence, despite the presence of common articulated valves and well-preserved shells.

In the sampled block, two individuals (four valves) of *Anadara amacula* are articulated among 29 detached valves (disarticulation ratio is 86.2%; Figure 2). Shells of *M. kurilensis* are often found in the upper part of or just above the *Anadara* shell lenses. Thirty-three articulated specimens and nine detached valves were found. Many of the *Modiolus* shells in the block are preserved in life position with commissure planes roughly vertical and shell long axes inclined at 60–70 degrees to the bedding plane (Figure 3). The shell surfaces are pristine, with no encrustation or boring.

Lenticular shell concentrations of *Anadara amacula* are considered to have served as the stable substrata on which the *M. kurilensis* colony developed. The presence of *Anadara* shells made bottom scouring and resultant reworking less common, thereby permitting colonization by *Modiolus*. Just above the *Anadara* lens, both articulated and detached specimens of *Modiolus* are scattered through the sediment. Articulated specimens do not retain their life orientation, and post-mortem disturbance is inferred at this stage (Figure 4-II), which preceded formation of the gregarious colony. This is probably because the *Anadara* shells were almost exposed on the sea floor or only very shallowly buried, so that *Modiolus* individuals were easily reworked on the sea floor.

In the following stage (Figure 4-III), a well-developed colony consisting of about 20 individuals was established. Most of the individuals in the colony are preserved in life orientation, as described above. The underlying shell layer was buried to a depth of c. 5–6 cm when the colony was formed, as inferred from the stratigraphic distance



**Figure 1.** Photograph of the colony of *Modiolus kurilensis*. A: plan view. B: cross-sectional view. Scale: the width of the photograph is about 35 cm.

between the shell layer and the reconstructed sea floor surface from the preserved life positions. This colony did not, however, continue to grow further (Figure 4-IV). *Modiolus* shells do not appear to facilitate successive colonization of the animal, probably because of the physical instability of a colony which is only supported by byssal threads. This is a major structural and taphonomic difference with much stable, cement-attached bivalve colonies formed by bivalves such as oysters.

Several other shell lenses in the same horizon occur nearby to the colony studied here. These shell lenses consist similarly of *Anadara amacula* and *M. kurilensis*, but *Modiolus* specimens were mostly detached and we could not find *in-situ* preserved specimens.

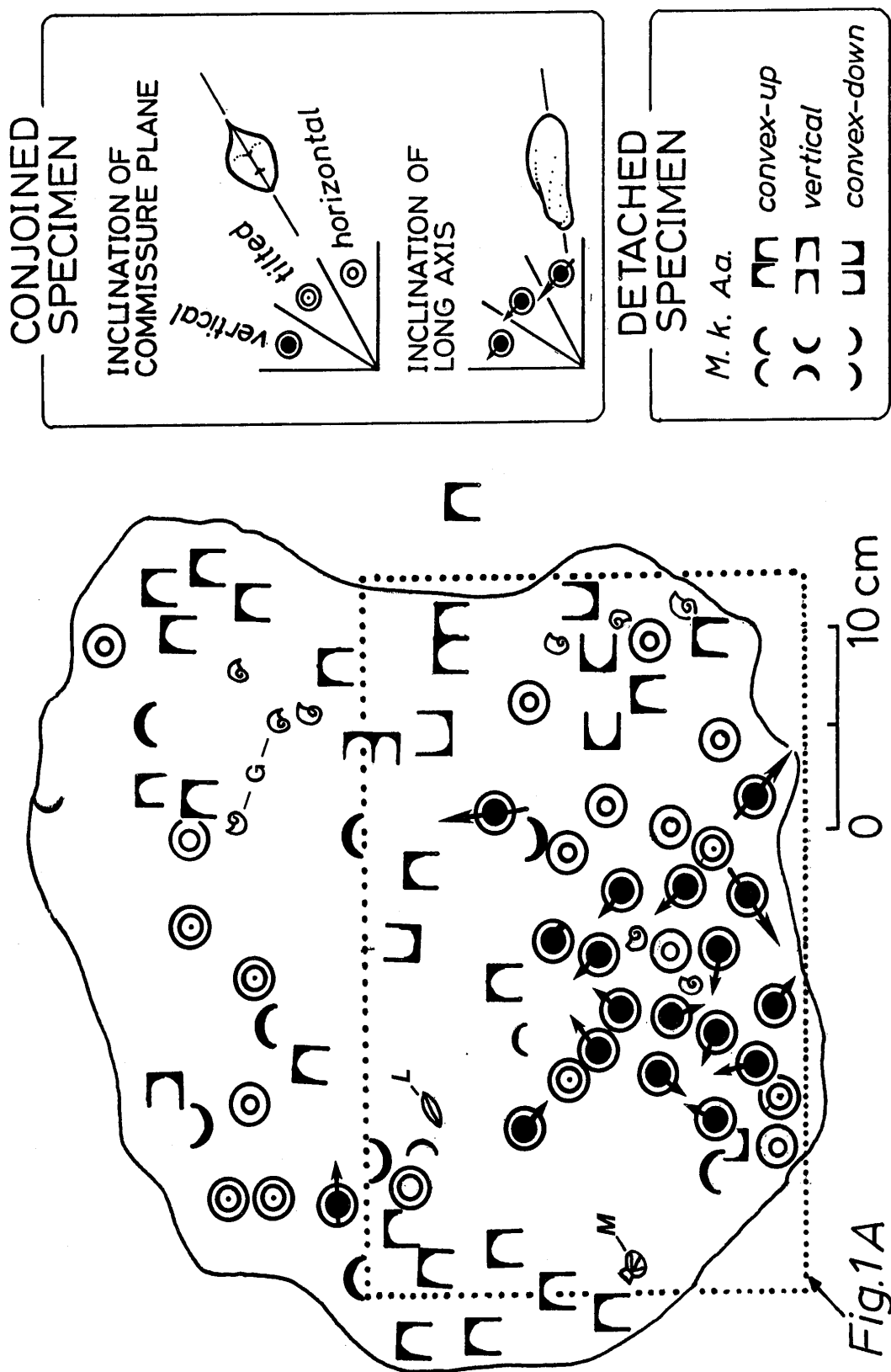
### Discussions

#### Ecology of living individuals

According to Habe and Ito (1965) and Okutani (1986), *M. kurilensis* is usually found byssally attached to rock surfaces. Okutani *et al.* (1989) reported collecting *M. kurilensis* with a dredge from a gravelly sandy bottom, but these authors also considered *M. kurilensis* to be a byssally attached, rocky-bottom dweller.

However, the shell morphology of *M. kurilensis* suggests otherwise. The shell has a moderately reduced anterior

adductor, and a cylindrical shell form with an anterior lobe, showing clearly that this species is a soft-bottom endobyssate species, as demonstrated by Stanley (1970, 1972) and Seed (1980). Epibyssate species, in contrast, have a highly reduced anterior adductor inside, a triangular shell form and no anterior lobe. Stanley (1970; 1972) stated that *Modiolus modiolus* normally lives with between half to two thirds of its shell buried in stable gravelly sand. Specimens sampled from the gravelly bottom reported by Okutani *et al.* (1989) further confirm this observation. Judging from Stanley's observation and his functional analysis, an epifaunal life habit on rocks as observed by Habe and Ito (1965) and Okutani (1986) is probably a fortuitous example, and the normal life habit of the species must be endobyssate. The presence of encrustation on the postero-dorsal surface of shells of extant specimens of *M. kurilensis* stranded on the beach near Usu-wan, Hokkaido (senior author's personal collection) also supports this interpretation. Specimens dredged from off Wakkanai, near the northern end of Hokkaido, show similar localized encrustation, suggesting an endobyssate life habit. Stanley (1972) stated that five out of the eight species of *Modiolus* which he studied live with partial or complete burial in a soft substratum, but may also occasionally be found attached epifaunally to hard substrata because of the vagaries of larval settlement,



**Figure 2.** Spatial distribution of individuals and their mode of occurrence of *Modiolus kurilensis* and *Anadara amicula*. Inclinations of commissure plane of conjoined specimens are shown as vertical, tilted and horizontal. For vertical specimen, inclination of the long axis is shown. Distribution of detached specimens is also illustrated. Note the convex-up shell orientation is common for *Anadara amicula* specimens. M.: a juvenile specimen of *Mizuhopecten tokyoensis hokurikuensis*, L.: an *in-situ* specimen of *Lucinoma annulata*, G.: *Gastropoda*, M. k.: *Modiolus kurilensis*, A.a.: *Anadara amicula*

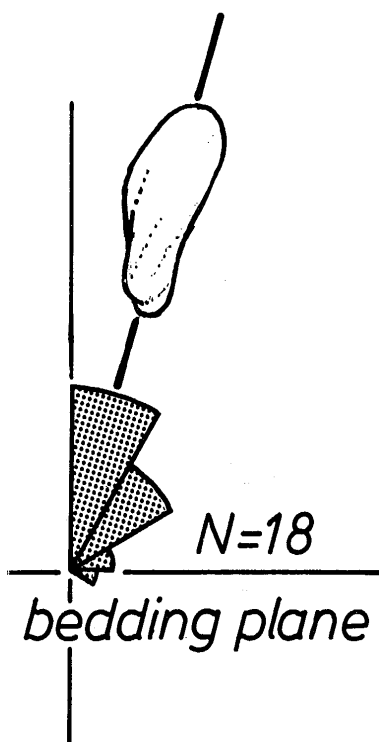


Figure 3. Preserved life orientation of *Modiolus kurilensis*.

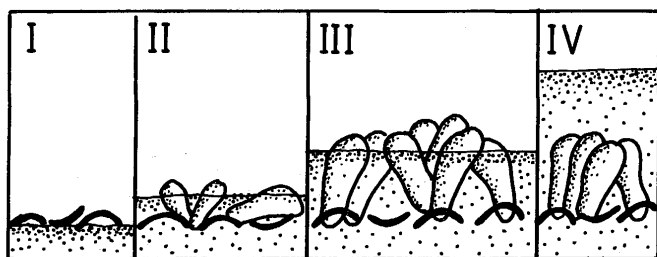


Figure 4. Schematic representation of stages of the establishment of the *Modiolus kurilensis* colony. I: shell pavement with only one layer thick shells, II: shelly substrate too shallowly covered by soft substrate to be colonized by *Modiolus*, III: shelly softground, most preferable condition for colonization by *Modiolus*, IV: shelly substrate too thickly covered by soft sediment to be colonized by *Modiolus*.

usually tending to lodge in crannies and crevices.

From the above discussion and our observation of the fossil colony, it is concluded that *M. kurilensis* is basically a soft-bottom dweller but that establishment of the colony required the initial presence of stable hard material in the substrata. The mode of life of this animal may thus be regarded as a transitional one between soft- and hard-bottom dwellers, and it is referred to as a shelly soft-bottom dweller or shell-gravel dweller.

#### Environmental conditions for and against colonization, and preservation of *Modiolus kurilensis*

*Modiolus kurilensis* is not common in the Omma Formation, according to the stratigraphic distribution chart of molluscs in the Omma Formation by Kitamura (1991b). This was also confirmed by our observation. Four different environmental factors are discussed below to explain this.

*Modiolus kurilensis* is a cold-water species. Climatic changes concomitant with the eustatic sedimentary cycles have therefore undoubtedly limited its distribution; the warmer periods represented by the middle unit of each cycle probably did not allow colonization by *M. kurilensis*. It is thus expected to occur only in cycle-bounding shell beds for which the marine climate is inferred to have been reasonably cold (Kitamura and Kondo, 1990).

Also ambient energy level may have affected the distribution of *M. kurilensis*. Kitamura (1991) reconstructed that the *Anadara-Clinocardium* associations in which the *Modiolus* colony was included were deposited in a cold water regime of water depth shallower than 20–30 m in an embayment. The environmental setting of the middle unit of the Omma Formation is inferred to have been of higher energy, as shown by the generally sandier sediment texture and common occurrence of open coast species such as *Macoma sector* and *Peronidia venulosa*. Though there is little direct information, it is likely that *M. kurilensis* prefers a sheltered environment, because of its endobyssate mode of life which needs substratum stability.

The physical condition of the substrate is considered important in the establishment of the *Modiolus* colony. Two different shelly substrata may be distinguished: shell pavement (Figure 4-I) and shelly softground (Figure 4-III). Shell pavement refers to a substratum carpeted by a layer of shells. This does provide a stable basis for many epibionts, but it is not suited for moderately large endobyssate bivalves like *M. kurilensis*. A shelly softground includes sufficient shell material within the soft substratum to allow colonization by *M. kurilensis*. We need, therefore, to distinguish these two different substratum conditions.

In relation to the above discussion, the mechanism of deposition of different shell beds may have determined the physical characteristics of the substrate and thus explain the relatively uncommon occurrence of *M. kurilensis* in the cycle-bounding shell beds of the middle Omma Formation.

Kitamura and Kondo (1990) demonstrated that the shell beds bounding sedimentary cycles in the Omma Formation were formed during low stands of sea level during 41 thousand-year glacio-eustatic cycles of the early Pleistocene. Formation of the shell beds is, therefore, the result of relatively long periods of deposition. However, Kondo and Kitamura (1988) have pointed out that the shell beds are often dominated by infauna, which only rarely show weathering or damage due to *Cliona* boring or encrustation by calcareous algae, barnacles or bryozoan. They therefore concluded that the formation of shell beds

involved rapid burial events. These observations are however not consistent with the general model for shell accumulation resulting from low rates of sedimentation. Perhaps the cycle-bounding shell beds were formed by repetitious storm deposition, and long-term environmental changes during lowstand of sea-level were thereby still recorded.

Accumulated shells were buried in well sorted very fine sand immediately after the emplacement event. Reworked shells were buried too deeply to be used as a basis to attach to with a byssus. Consequently, a shelly soft bottom condition was not available for *Modiolus* during formation of the shell beds. In contrast, the shell lenses of *Anadara* in the lower unit of the Omma Formation are not associated with a rapid burial event and colonization was possible.

Kidwell and Jablonski (1983) recognized two types of shell concentration associated with low net sedimentation; (i) undisturbed reduced sedimentation, which permits nearly continuous maintenance of a shelly substratum (low total sedimentation), and (ii) repeated physical disturbance, producing a shell concentration containing both epifaunal and infaunal taxa (high total sedimentation). The basal shell bed in the middle unit of the Omma Formation is understood as a further extreme type of higher total sedimentation, in which almost no shelly substratum appeared on the surface during formation of the shell bed (highest total sedimentation).

In summary, it is concluded that a shelly softground which could be colonized by endobysate bivalve was only rarely available on the inner shelf muddy sand bottom during deposition of the Omma Formation.

Lastly preservation is considered to be important in producing the observed pattern of stratigraphic distribution of *Modiolus* shell and colonies. Even if a *Modiolus* colony was successfully established during deposition of a cycle-bounding shell bed, it is unlikely to have been preserved *in situ*, because bottom sediment reworking to a depth of 10–20 cm constantly occurred. In fact, reworking may have reached 50 cm depth, as inferred from the analysis of preservation of bivalve life positions. The relatively uncommon scattered shells of *M. kurilensis* which occur in the Omma Formation may represent reworked and transported shells during such high energy events.

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