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Preserved Life Orientations of Soft-Bottom Infaunal Bivalves: Documentation of Some Quaternary Forms from Chiba, Japan

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Abstract Life orientations of 19 species of soft-bottom infaunal bivalves preserved in the Quaternary of Chiba, Japan, are described, and some are compared to the observation of living specimens. New ecological information was given to bivalves including deep-burrowing lucinaceans and a periplomatid which were ecologically little known. The orientations preserved in the strata agree with the normal feeding orientations in most cases. There are, however, a few examples showing hydrodynamically unstable orientations which are also different from the normal life orientation.

Most of the bivalves described are deep burrowers or those living in protected environment, where water agitation is limited and muddy substrata dominate. This indicates that depths of shell burial and depths of physical disturbance, such as sea-bottom erosion, are the most important factors determining preservation of the bivalve life position. Bioturbation may have played some role in changing the orientation of dead bivalves from the original life position especially in the case of small bivalves. Compaction effect may also have modified the original orientation, increasing the inclination of elongated forms.

Key words: life orientation, bivalve, taphonomy, Quaternary.

Recognition of preserved life positions of fossils has long been a common practice for geologists when they are engaged in paleoenvironmental reconstructions, because they are the only definite evidence showing *in situ* burial. Also, an analysis of bivalve life orientations preserved in shell beds has been shown to be a practical tool in interpreting depositional and erosional processes of shell beds (Kondo, 1987a; 1989). Observation of presreved life position is thus important for taphonomists and paleoecologists. In addition, position of benthos within the substratum is considered a clear expression of its ecological adaptation to the physical environment (Stanley, 1970). The description of preserved life positions of ecologically little-known living species would contribute to understanding their life habits, which are difficult to observe for the living specimens in nature.

Descriptions of preserved position of fossil benthos in the strata therefore, are a reliable source of information on which future studies can be based. Precise descriptions of preserved bivalve life positions are, however, very scarce, except for the descriptions of Jurassic bivalves by Fürsich (1980) and occasional descriptions in some paleontology textbooks (*e.g.,* Chinzei, 1973).

This paper deals with the first systematic description of the orientations of the infaunal bivalves preserved in the Quaternary, distributed in Chiba, Central Japan. Also, I will discuss taphonomic and paleoecologic implications of the preserved life positions of the bivalves.

Life Position of Soft-Bottom Infaunal Bivalves

Each species of soft-bottom infaunal bivalves can assume different positions within the substrata according to different needs in life. Figure 1 shows various orientations assumed by a common Japanese bivalve, *Ruditapes philippinarum* (Adams et Reeve), based on my observation of the living forms on the sand flats in Chiba: a physically stable orientation on being exposed on the sea-botttom (A), an orientation in reburrowing (B; "erect probing orientation", Stanley, 1970), an orientation in the course of burrowing (C), a feeding orientation (D; normal feeding position), and an orientation in escaping on anastrophic burial (E; "inverted erect probing orientation", Krantz, 1974). All these orientations have a chance of being preserved in the stata.

Life position is, in general, defined as the normal feeding position (Stanley, 1970). It is thus important to consider the siphon disposition in determining the life position of a bivalve species. Many examples of bivalve life position can be best understood as the easiest way of positioning

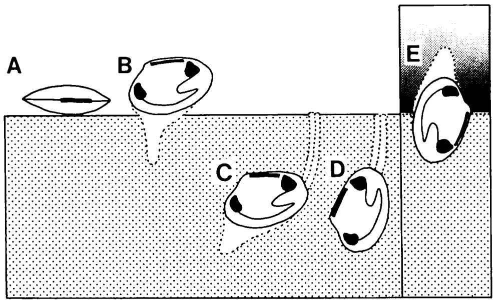

Fig. 1. Schematic representation of various orientations assumed by a soft-bottom infaunal bivalve *Ruditapes philippinarum* in life. For explanation, see text.

their siphons or corresponding organs for feeding, as discussed and illustrated by Stanley (1970: fig. 34).

Table 1. List of bivalve species for which life position is documented in this paper.

Solemya tokunagai Yokoyama
Conchocelle bisecta (Conrad)
Lucinoma annulata (Reeve)
Lucinoma aokii Hirayama
Anodontia sternsiana Oyama
Clinocardium braunsi (Tokunaga)
Saxidomus purpuratus (Sowerby)
Callithaca adamsi (Reeve)
Callista chinensis (Holten)
Paphia undulata (Born)
Dosinella penicillata (Reeve)
Dosinorbis japonicus (Reeve)
Clementia papyracea (Gray)
Raeta pellicula (Reeve)
Tresus keenae (Kuroda et Habe)
Solen krusensterni Schrekck
Panopea japonica A. Adams
Mya arenaria oonogai Makiyama
Periploma otohimeae Habe

Field Observation

Shell orientations of conjoined bivalve specimens were measured for 19 bivalve species (Table 1) at the ten outcrops in Chiba Prefecture (Table 2).

Bivalve life position includes depth of shell burial and shell orientation as defined by Stanley (1970). Depth of shell burial cannot, however, be readily observed in the fossil record, and was not inferred in this study. Shell orientation is expressed as the inclination of the commissure plane of conjoined bivalves to the bedding, and the inclination of the long axis, or antero-posterior axis, of the shell to the bedding. In some example, the inclination of the long axis will also be expressed as an angle between the long axis and the vertical from the bedding. These two parameters were used for measurements. Azimuthal orientation was not measured. In the following descriptions, an adjective "vertical" will be used as implying

Table 2. Observation sites for preserved life position of bivalves.

locality (all in Chiba Prefecture)	age	sediment	described species
Taitozaki, Misaki-machi: the same locality of O'Hara (1974)	Holocene	mud	*Mya arenaria, Anodontia stearnsiana*
Kinu, Futtsu-shi,	Holocene	pebbly mud	*Paphia undulata, Dosinella penicillata*
Sakurai, Kisarazu-shi: Loc. 1 of O'Hara et al. (1976)	Late Pleistocene Kioroshi Fm	pebbly mud	*Dosinella penicillata, Panopea japonica*
Otake, Immba-mura	Late Pleistocene Kioroshi Fm	very fine sand	*Panopea japonica,*
Yoshitaka, Immba-mura	Late Pleistocene Kioroshi Fm	very fine sand	*Panopea japonica, Raeta pellicula*
Tsurumaki, Immba-mura	Late Pleistocene Kioroshi Fm	very fine sand	*Raeta pellicula*
Nagayoshi, Sodegaura-machi: Loc. 21 of Tokuhashi & Endo (1984)	Middle Pleistocene Kiyokawa Formation	pebbly sand	*Panopea japonica, Tresus keenae, Saxidomus purpuratus, Dosinorbis japonicus, Lucinoma annulata, Callista chinensis, Clementia papyracea, Clinocardium braunsi*
Mariyatsu, Kisarazu-shi: Loc. 55 of Tokuhashi & Endo (1984)	Middle Pleistocene Yabu Fm	very fine sand	*Panopea japonica, Tresus keenae*
Dai, Kimitsu-shi: 400m NE from Loc. 48 of Tokuhashi & Endo (1984)	Middle Pleistocene Jizodo Fm	sandy mud	*Saxidumus purpuratus, Callithaca adamsi*
Tabi, Ichihara-shi: close to Loc. 137 of Tokuhashi & Endo (1984)	Middle Pleistocene Kasamori Formation	silt	*Periploma otohimeae*
Kawayatsu, Kimitsu-shi	Middle Pleistocene Kakinokidai Formation	silty sand	*Solemya tokunagai, Lucinoma aokii, Conchocele bisecta*

the commissure plane is oriented vertically to the bedding.

Results

Preserved life orientations are described in the following section for each species. Information of the life orientation of the living individuals of the identical species is given for comparative purpose.

Solemya tokunagai **Yokoyama**

Life habit. This species has a large cylindrical shell, more than 10cm long. Living specimens are found in muddy substrata of the upper bathyal zone in the northwestern Pacific (Habe and Ito, 1965). The life orientation of this species has not been described. Stanley (1970) reported that *Solemya velum* Say, a much smaller species than *S. tokunagai,* makes a Y-shaped burrow and stays in the lowest portion of the U-shaped segment of the burrow. There are, however, no workers observed such burrows for other *Solemya* species (Yonge, 1939; Owen, 1961).

Mode of fossil occurrence. Seven specimens were observed and measured in the silty sand of the middle Pleistocene Kakinokidai Formation at Kawayatsu (Table 2). The shell orientation is a vertical, anterior up orientation, with the long axis 20° to 35° from the bedding. This is one of the rare examples of an orientation with the anterior portion upward. The smallest individual was found vertical, with the long axis horizontal, and one of the adult individuals was oriented vertically, with the long axis perpendicular to the bedding.

It is uncertain whether *S. tokunagai* was living in a burrow, like *S. velum.* There are no burrow-like structures observed around the *in-situ S. tokunagai* specimens. The inclined long axis of the shell does not seem to be consistent with the orientation within the U-shaped segment of the burrow as observed by Stanley (1970). It is unclear what the anterior up shell orientation means and additional observations of living specimens is needed.

Conchocele bisecta **(Conrad)**

Life habit. This species is a large-sized thyasirid in the North Pacific. The life position has not been described. Kauffman (1967) illustrated the life position of a member of the same family, *Thyasira flextuosa* (Montagu) as a vertical, beak up orientation, based on the ecological description by Allen (1958).

Mode of fossil occurrence. Eleven individuals were observed in the silty sand of the middle Pleistocene Kakinokidai Fomration at Kawayatsu (Table 2). Most of the individuals are oriented vertically, with the antero-dorsal part upward. This orientation is roughly similar to, but clearly different from the beak up orientation illustrated by Kauffman (1967) for *T. flextuosa.* The preserved orientation of the antero-dorsal part upward seems to be the easiest way to position inhalant mucus tubes upward. Direct observation of living specimens in the substratum is necessary to determine the normal life position of *Thyasira* species.

Lucinoma annulata **(Reeve)**

Life habit. This is a small lucinid species living in the western Pacific. It is *a common* bivalve distributed in muddy substrata in protected environments, but its life position and other ecological properties have not been described. Stanley (1970) described life positions of some lucinids, including *Codakia orbicularis* (Linnaeus), *Phacoides pectinatus* (Gmelin), *Phacoides muricatus* (Spengler) *Anodontia alba* Link and *Lucina pensylvanica* (Linnaeus). They were observed to be buried in the substrata with their beak-upward. Only *L. pensylvanica* was oriented with its antero-dorsal portion wpward.

Mode of fossil occurrence. Five individuals were observed in the very fine sand of the Late Pleistocene Kiyokawa Formation at Nagayoshi (Table 2). Four out of the five individuals were oriented vertically, with their antero-dorsal por-

Lucinoma annulata

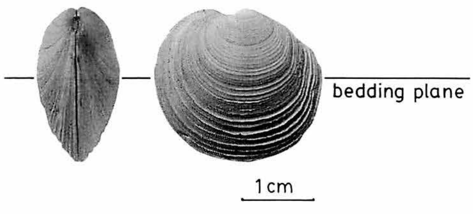

Fig. 2. Preserved life orientation of *Lucinoma annulata.* Note that the antero-poterior axis is inclined, so that the anterior part is oriented upward.

tion upward (Fig. 2). This orientation is similar to that of *L. pensylvanica,* as described by Stanley (1970).

***Lucinoma aokii* Hirayama**

Life habit. This is an extinct lucinid, with a large shell. Information on life positions of similar lucinid species are available from Stanley (1970) as stated in the preceding section.

Mode of fossil occurrence. Orientations of 14 individuals of this species were measured in the silty sand of the middle Pleistocene Kakinokidai Formation, at an outcrop in the tunnel of Kawayatsu, Kimitsu-gun (Table 2). Thirteen out of the 14 individuals were conjoined, and nine out of the 13 conjoined individuals were oriented vertically to the bedding. This indicates that post-mortem reworking or bioturbation was minimal during deposition of this shell bed, and nearly all the vertical, conjoined individuals can be regarded as being in their life position. Six out of the nine vertical, conjoined individuals are oriented with the antero-dorsal part upward (Fig. 2). This orientation is interpreted as the preserved normal feeding orientation of this species.

***Anodontia stearnsiana* Oyama**

Life habit. This is a thin-shelled, well-inflated lucinid, in muddy substrata in protected bay. Life orientation of this species has not been observed. Stanley (1970) described the life position of a member of the same genus, *Anodontia alba.* It was observed to be oriented vertically, with the beak upward, at depths of more than 20cm.

Mode of fossil occurrence. Only two individuals were found in the Holocene deposits distributed in the Taitozaki (Table 2), near the southern end of Kujukuri beach. Preserved life position is vertical, with the beak position upward (Fig. 3).

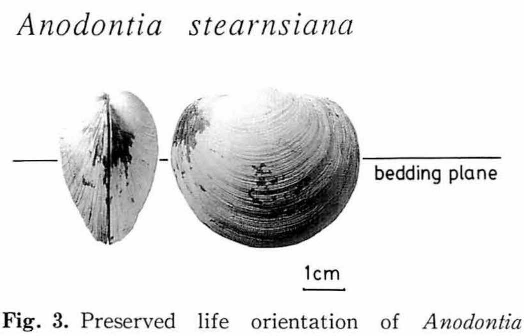

Fig. 3. Preserved life orientation of *Anodontia stearnsiana.* The antero-posterior axis is nearly horizontal.

***Clinocardium braunsi* (Tokunaga)**

Mode of fossil occurrence. This is one of the rare examples of an extinct Quaternary bivalve occurring in the middle to late Pleistocene shallow marine deposits in southern Kanto. It has a large shell with strongly projecting radial ribs. This species is not rare, but conjoined specimens are seldom found. Only a single specimen of 10.5 cm shell length was found in the pebbly sand of the basal part of the Kiyokawa Foramtion at Nagayoshi (Table 2), and it was oriented vertically, with the posterior portion upward (Fig. 4). The orientation is consistent with the life orientation of many living cardiids (*e.g.,* Stanley, 1970).

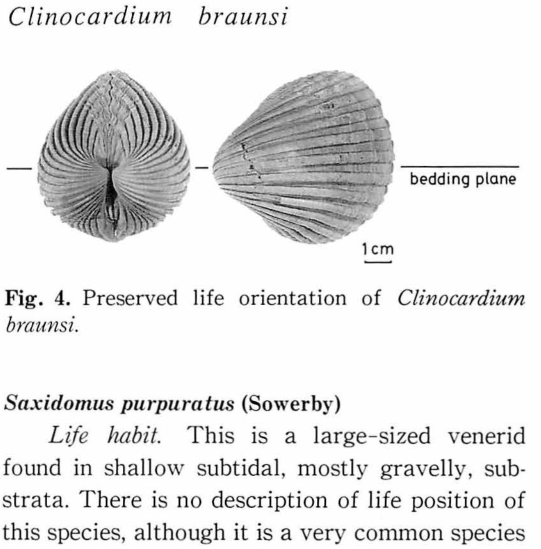

Fig. 4. Preserved life orientation of *Clinocardium braunsi.*

***Saxidomus purpuratus* (Sowerby)**

Life habit. This is a large-sized venerid found in shallow subtidal, mostly gravelly, substrata. There is no description of life position of this species, although it is a very common species around Japan. As the pallial sinus is deep, this species is probably a deep burrower.

Mode of fossil occurrence: Observations were made in the sandy silt of the middle Pleistocene Jizodo Formation at Izumiyatu, in the pebbly sand of the late Pleistocene Kiyokawa Formation at Nagayosi, and in the basal part of the Holocene deposits at Taitozaki (Table 2). At the former two localities, this species occurs in a vertical, posterior-up position in soft sediments (Figs. 5, 6). At Taitozaki, this species occurs within burrows in semi-consolidated basement mudstone of deep sea origin in the Kiwada Formation . A

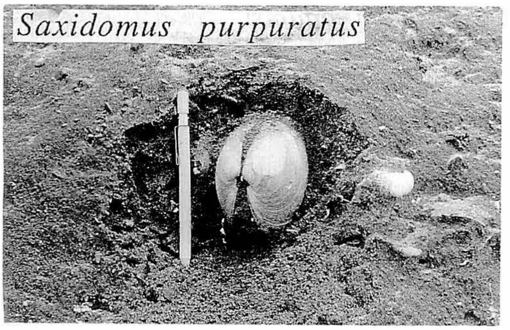

Fig. 5. A field photograph of *Saxidomus purpuratus* preserved in life position in the gravelly sand of the middle Pleistocene Kiyokawa Formation at Nagayoshi, Sodegaura-machi. The bedding plane is horizontal.

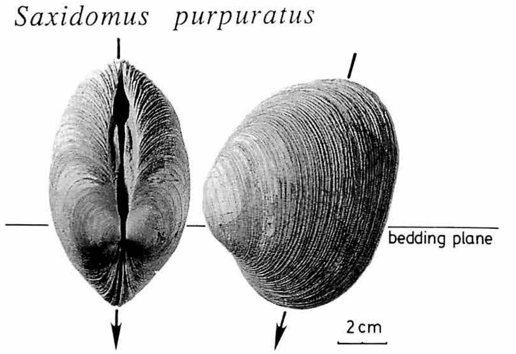

Fig. 6. Preserved life orientation of *Saxidomus purpuratus*.

similar occurrence, showing a boring habit of this species, was reported by Matsushima and Ohshima (1974) and Matsushima and Yoshimura (1979).

Dosinorbis japonicus (Reeve)

Life habit. This is a common venerid, living in lower intertidal and shallow subtidal sandy substrata in Japan. Kondo (1987b) described the life position of this species, as a vertical, posterior-up orientation. Depth of burial ranges from 2 to 15cm.

Mode of fossil occurrence. Observation was made in the basal part of the Kiyokawa Formation at Nagayoshi (Table 2). Conjoined specimens of this species occur parallel to the bedding plane in most cases. Only three out of more than 30 conjoined specimens are found vertical to the bedding. Two specimens show probable life orientations; one of the two specimens a juvenile speci-

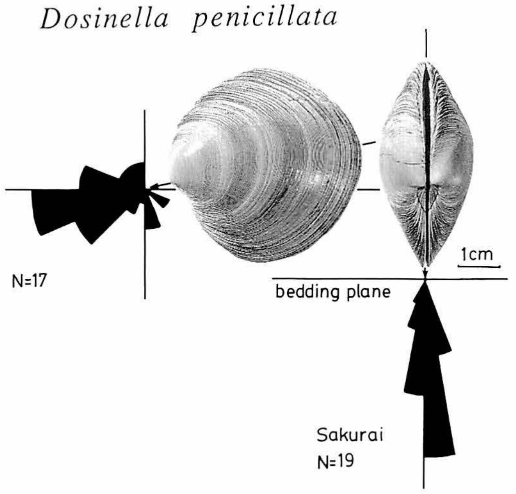

Fig. 7. Preserved life orientation of *Dosinella penicillata.*

men of 3.3cm shell length is oriented roughly vertical, with the posterior upward. The remaining specimen is oriented vertical, with the anterior-upward. It is unclear whether this orientation is an orientation during escape from a burial event or a fortuitous life orientation.

Dosinella penicillata (Reeve)

Life habit. This is a common venerid living in the muddy substrata in protected bay around Japan. The life position of this species has not been decribed.

Mode of fossil occurrence. This species is commonly found in life position in the inner bay muddy deposit, which is common in the Holocene drowned valley in Chiba Prefecture. Observations were made in two localities: the Holocene mud exposed along the river side of Iwasegawa, at Kinu and the late Pleistocene Kioroshi Formation at Sakurai (Table 2). At Kinu, 26 conjoined specimens were observed, out of which 19 were vertical, and the rest were oblique or horizontal. Beak positions were variable among vertically oriented specimens; nine specimens were in posterior-up orientation, 10 were in beak-down orientation. At Sakurai, however, beak positions were slightly different: most of the specimens were oriented with their posterior and beak upward, and beak-down positions were much rare (Fig. 7).

Callista chinensis (Holten)

Life habit. This is a common venerid, living

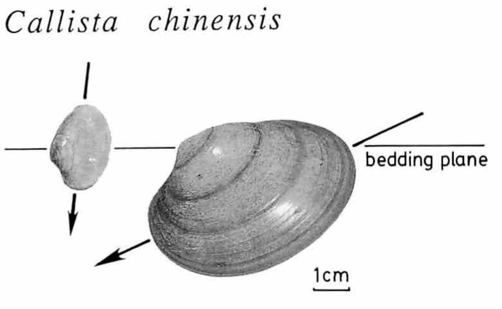

Fig. 8. Preserved life orientation of *Callista chinensis*. Note the difference in the inclination of the long axis between adult and juvenile specimens.

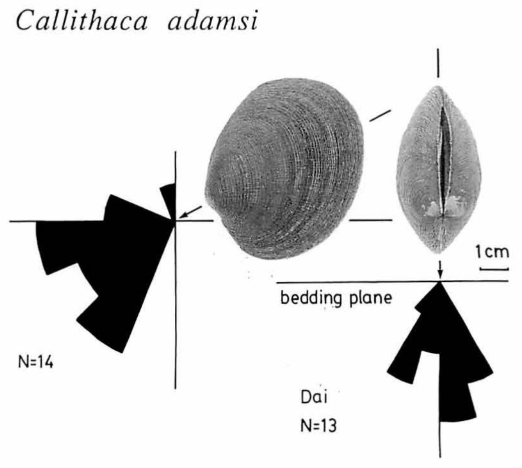

Fig. 9. Preserved life position of *Callithaca adamsi*.

in the upper sublittoral zone in the western Pacific. Life position of this species was observed in the laboratory using living specimens collected from Maizuru Bay, north of Kyoto: It is oriented vertically, with the beak to posterior portion upward. The Long axis of the shell was tilted 40°-50° from the horizontal.

Mode of fossil occurrence. Observation was made in the basal part of the Kiyokawa Formation at Nagayoshi (Table 2). This species occurs mostly parallel to the bedding plane. Only three specimens were found vertical to the bedding; a juvenile specimen of 1.5cm shell length was oriented roughly vertically, with the posterior portion upward. The long axis was nearly vertical. Another specimen of 6.2cm shell length was oriented roughly vertically, with the beak-posterior portion upward. The long axis was tilted anteriorly 20° from the horizontal (Fig. 8). The remaining specimen was oriented vertical, with the anterior-upward.

Paphia undulata **(Born)**

Life habit. This species commonly occurs in shallow subtidal muddy substrata in Japan. The life position of this species was observed in the laboratory, using specimens from Tokyo Bay: It assumes vertical, posterior-up orientation, with the long axis slightly tilted.

Mode of fossil occurrence. Only a single specimen was found in life position in the Holocene mud bed along the River Iwasegawa, Futtsu-shi, Chiba (Table 2). The preserved life position is a vertical, posterior-up orientation, with the long axis tilted 35°-40° from the vertical.

Clementia papyracea **(Gray)**

Life habit. This is a thin-shelled, well inflated venerid. The life position of this species has not been described. A deep burrowing habit is inferred from the deep pallial sinus.

Mode of fossil occurrence. A single individual was found in life position in the Late Pleistocene Kiyokawa Formation at Nagayoshi (Table 2). The preserved life orientation is vertical, posterior-up, the same as the orientation commonly assumed by most infaunal suspension-feeding bivalves.

Callithaca adamsi **(Reeve)**

Life habit. This is a medium-sized venerid, common in northern Japan. The life orientation of this species has not been described. It is, however, safely inferred that this species assumes a conventional, vertical, posterior-up life orientation.

Mode of fossil occurrence. Fourteen conjoined specimens were observed in the Izumiyatu fossil bed of the Jizodo Formation (Table 2). All of the specimens were found in a hydrodynamically unstable, vertical or oblique position. Most of them show posterior-up orientations (Fig. 9). Inclination of the commissure plane varies more than other examples described in this paper. Beak positions are also variable. A single specimen was found vertical, with the anterior upward.

Raeta pellicula **(Reeve)**

Life habit. This is a thin-shelled, well-inflated mactrid. The life orientation of this species

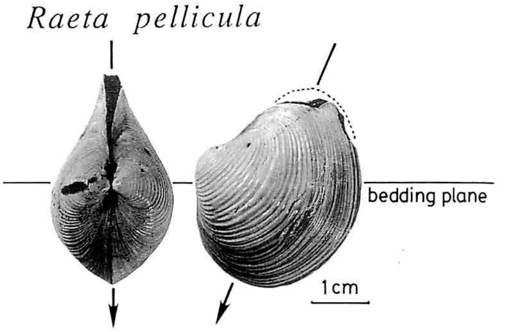

Fig. 10. Preserved life orientation of *Raeta pellicula.*

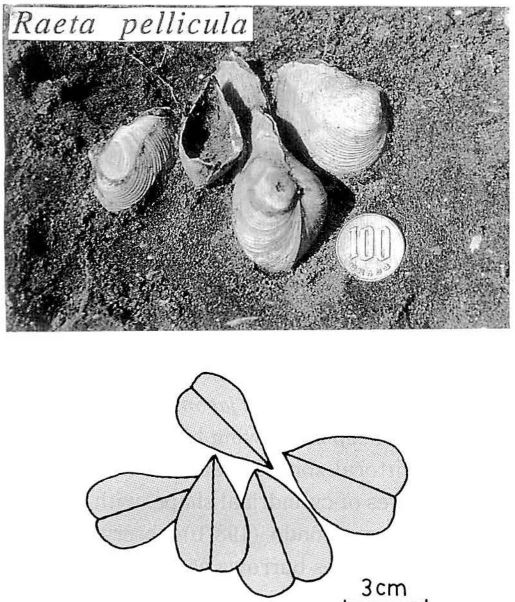

Fig. 11. A field photograph showing colonial occurence of *Raeta pellicula* (upper), and a sketch in plan view (lower).

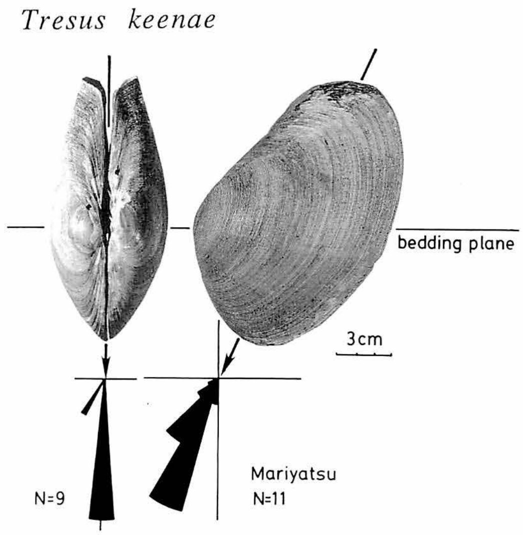

Fig. 12. Preserved life orientation of *Tresus keenae.*

has not been described.

Mode of fossil occurrence. Nine specimens were found in their life position at Yoshitaka, Tsurumaki and Nagayoshi (Table 2). Preserved life position of this species is vertical, with their posterior upward. Its long axis is tilted (Fig. 10). An unusual patchy distribution was found in the Kioroshi Formation at Tsurumaki, where five individuals were found in a small colony (Fig. 11). Each individual is oriented so that their ventral margins are close to each other.

Tresus keenae (Kuroda et Habe)

Life habit. This is a deep - burrowing bivalve, with very large shells. The life position of this species has not been observed, probably due to the difficulty of observaiton of deep burrowing bivalves. Pohlo (1964) described a vertical, long-axis-inclined living position for *Tresus nuttalli* (Conrad), a similar northeastern Pacific species, on the mud flats in Tomales Bay, California. An adult specimen shows an inclined life position, while it is nearly vertical in juveniles. Stanley (1970) also found a similar phenomenon, describing the life position of the living individuals belonging to the same family, *Mactra fragilis.*

Mode of fossil occurrence. Fifteen individuals were observed in the very fine sand of the middle Pleistocene Yabu Formation at Mariyatsu (Table 2), out of which 11 were found in a vertical life position. The life position of this species is similar to that of *Panopea japonica* and *Mya arenaria,* but it differs in its distinctly inclined long axis from the vertical. The long axis of this species inclined 30° on the average, although it varies from 0° to 70° (Fig. 12).

Solen krusensterni Schrenck

Life habit. This is a common solenid species, found in shallow subtidal settings in Japan. There is no description of the mode of life of this species. It is, however, possible to infer the life habit of this species by analogy with a similar species *Solen strictus,* a common intertidal species described by Frey *et al.* (1988) from Korea. *Solen strictus* lives in a deep vertical burrow lined with

Fig. 13. A field photograph of *Panopea japonica* preserved in life position in the very fine sand of the middle Pleistocene Yabu Formation.

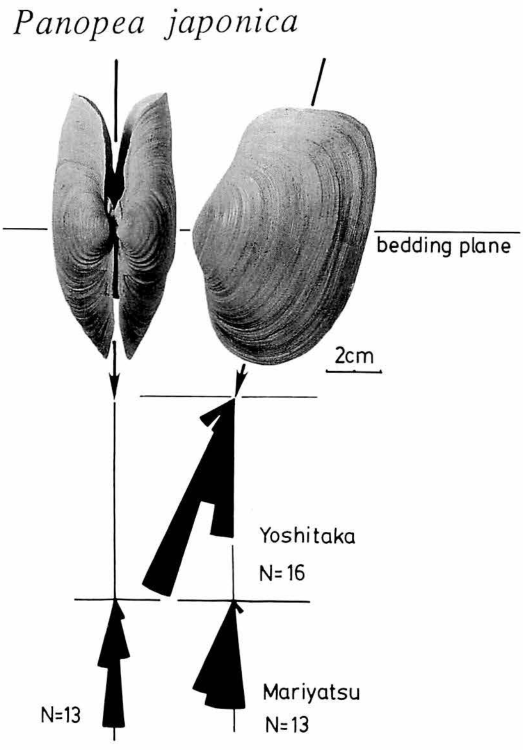

Fig. 14. Preserved life position of *Panopea japonica.*

mud, up to 50 cm long. In general, the burrows are tilted about 15° from the vertical.

Mode of fossil occurrence. Several individuals were found in their life position at Mariyatsu and Nagayosi (Table 2). The preserved life position of this species is vertical, posterior-up, with its long axis about 20° from the vertical. Burrows were not recognized around the *in situ* specimens.

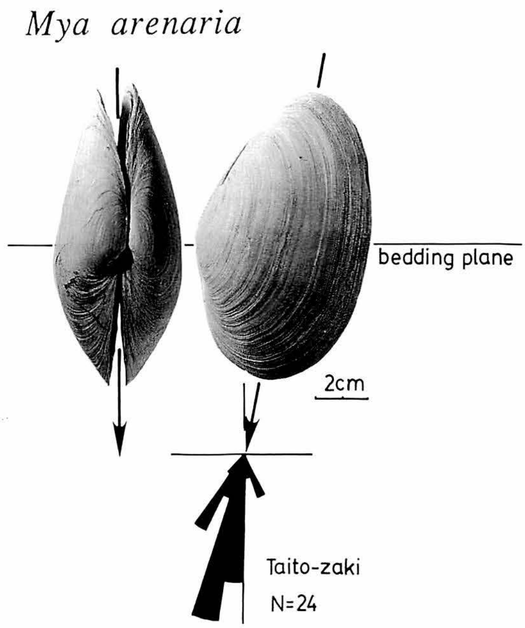

Fig. 15. Preserved life position of *Mya arenaria oonogai.*

***Panopea japonica* A. Adams**

Life habit. Panopea japonica is an almost immmobile, deep-burrowing bivalve, living in the upper sublittoral zone. It has well-inflated, thin-shelled valves of cylindrical shape, with pedal and siphonal gapes. Kondo (1987b) observed a specimen of this species burrows as deep as four times shell length in the laboratory. Inclination of the long axis has not been observed.

Mode of fossil occurrence. This is one of the commonest bivalve species found in its life position in the Quaternary deposits of Chiba Prefecture. Observations were made at the middle to late Pleistocene deposits at Nagayosi, Otake, and Mariyatsu. Five out of six individuals of this species are found in vertical life positions in pebbly sand at Nagayosi. Similarly, 14 out of 16 at Mariyatsu, and 13 out of 16 at Otake are found in their life position.

Preserved life orientations of this species are vertical, posteriorup orientation, with the truncated posterior portion parallel to the bedding. Inclination of the long axis of the shell varies from −5° to 25° anteriorly from the vertical (Fig. 13 and 14). The slightly tilted shell orientation is interpreted as a result of vertical disposition of the long siphon.

Mya arenaria oonogai **Makiyama**

Life habit. This is a deep-burrowing bivalve, living in intertidal sand-mud flats. The life position of living individuals of this species has been observed by some authors (Medcof, 1950; Goshima, 1982). According to them, this species is buried in the substratum with its long axis nearly vertical or slightly tilted ventrally.

Mode of fossil occurrence. Twenty fjve individuals of this species were observed at Taitozaki (Table 2), 24 of which were found preserved in a vertical, posteriorup life position. Inclination of the long axis ranges from -20° to 40°, but most of the measurements fall within the range of 0° to 25° (Fig. 15).

The orientation of the long axis of the fossil examples appears to be more inclined as compared to those observed for living individuals.

Periploma otohimeae **Habe**

Life habit. This is a deep water periplomatid species living around Japan. Ecological observation of this species or other species of the genus have not been made.

Mode of fossil occurrence. Twenty five individuals of this species were observed in the middle Pleistocene Kasamori Formation, at Tabi (Table 2). They were all oriented parallel to the bedding, with their right valve upward. This is safely interpreted as their life position, in spite of being similar to the hydrodynamically stable orientation on being exposed on the sea bottom.

The horizontal life position of this species may indicate deposit-feeding life habit, being similar to most tellinids. A horizontal life position within the substratum has been interpreted as an adaptation to active movement, which is necessary for deposit-feeding (Holme, 1961; Stanley, 1970).

Discussion: Taphonomic and Paleoecologic Implications of Preserved Life Positions of Soft-Bottom Infaunal Bivalves

The information on the preseved life positions can provide insight into many studies including taphnomy and paleoecology of the bivalves. To clarify the meanings of preserved life position, it is appropriate to examine factors determining the presrevation.

The most important factor determining the preservation of life position is depth of shell burial within the substratum, as suggested by Fürsich (1980) and Kondo (1987a). Most of the bivalve species described above are deep burrowers. The described life positions of shallow burrowers, such as those of *Clinocardium braunsi*, may be taken for fortuitous examples. Shallow burrowers are usually preserved in reworked, hydrodynamically stable positions in shallow-sea sediments like those of the Shimosa Group.

Kondo (1987a) attributed selective preservation of life position of deep-burrowing bivalves, to sea floor erosion probably of storm origin. The depth of erosion in shallow-sea sandy botttom was estimated to be 15-20cm from the sediment surface. Only extremely deep burrowers, such as *Panopea japonica* and *Tresus keenae,* which are buried more deeply, are usually preserved in life positions. Most bivalves buried at shallower positions are reworked on the sea floor and oriented in hydrodynamically stable positions.

Another factor controlling preservation of life position relates to environmental conditions, such as depth of storm erosion. In general, the depth of storm erosion is greater, as the environment becomes shallower and being more exposed to open sea.

Two bivalves *Dosinorbis japonicus* and *Dosinella penicillata* are preserved in a contrasting manner, in spite of the similar shell morphology and similar depth of burial. It is common for *D. penicillata* to be preserved in life position, while *D. japonicus is* rarely preserved in life position. *Dosinella penicillata* lives in the shallow-sea mud bottoms of embayment. In contrast, *D. japonicus* lives in sandy bottoms in similar shallow seas. Diferent depth of erosion is probably the main factor producing their contrasting modes of preservation.

Bioturbation effects are interpreted as being negligible in the cases where the shells are large enough: Bivalves with shells larger than 3-5cm are found in their life orientation or physically stable reworked orientation, with only small variations, while small bivalves less than 3cm are susceptible to probable bioturbation effect. Compaction may have modified the original life positions, as Fürsich (1980) pointed out. In some individuals, minor differences were recognized between living and fossil life positions, *e.g.,* in the inclination of the long axis of large-sized, deep

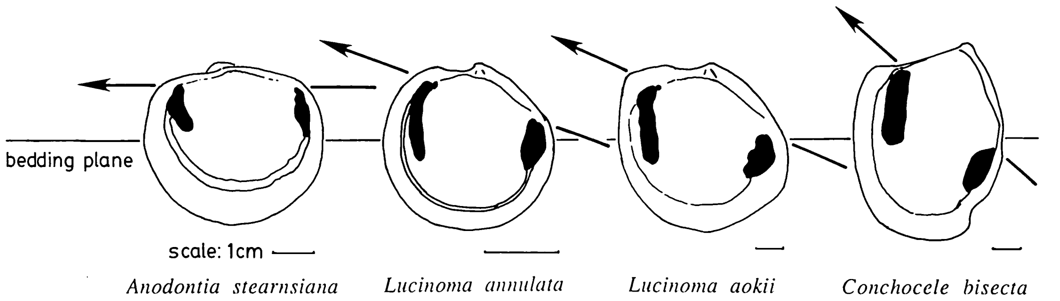

Fig. 16. Life orientations of some lucinaceans. Schematic drawings of left lateral view. A: *Anodontia stearnsiana,* B: *Lucinoma annulata,* C: *Lucinoma aokii,* D: *Conchocele bisecta.* Each arrow shows antero-posterior axis.

burrowing bivalves, such as *Panopea japonica, Tresus keenae* and *Mya arenaria.* The inclination of their long axis was observed to be larger than that observed in living specimens. Sometimes their shells were found nearly horizontal, with the commissure plane still being vertical.

As discussed above, preservation of life position is strongly influenced by the environmental conditions as well as the ecological characteristics of the species. If the life orientation and depth of burial are reconstructed properly, systematic analysis on preservational trends in the bivalve life position will provide information on the paleoenvironments and diagenetic conditions, which cannot be obtained from other conventional observations (Kondo, 1987a; 1989). Conversely, if we compare the preservational condition of bivalve life position in the same shell bed, the observed difference can be taken for the difference of autoecology of each bivalve.

Another implication of the preserved life position include causes of death of the animal, as suggsted by Ager (1963, p.83). Observed life positions of soft-bottom infaunal bivalves are mainly consistent with those observed on living individuals or those inferred by analogy with similar species. No serious discrepancies were found between fossil and living life positions. In most examples, the observed orientation agree well with the normal life position, that is, the feeding orientaiton. There are, however, a few examples showing a hydrodynamically unstable orientation, but different from normal life orientation for such species as *Dosinorbis japonicus, Callista chinensis, Callithaca adamsi.* The anterior-up orientation is similar to the inverted erect probing orientation assumed during escape upon anastrophic burial. It is, however, uncertain whether the orientations were assumed due to such a burial event. Such escape orientations can be properly recognized only when most of the fossil individuals concerned are in the anterior-up orientations within a bed with characteristic sedimentary features of rapid burial.

Preservation in normal life position indicates that the animal died in normal feeding orientation; it died neither of attack by predators nor of such physical disturbances as those found during periods of severe storms. After death, the position and orientation have not been shifted or rotated by biological or physical agents, and have not been exposed to erosion.

Preserved life orientation of bivalves is well worth being documented, also because it is one of the important expressions of the ecology of the animal, particularly for extinct species. As an example, life positions of lucinaceans are briefly discussed below from the viewpoint of relations among shell form, life position and the ecology.

Stanley (1970) found some relationships between shell form and life position in bivalves of various life habits including soft-bottom infaunal dwellers. Some examples described above can add new information on this field of study.

Life orientations of lucinacean bivalves appear to be grouped into two types: One is a beak-up orientation shown by *Anodontia stearnsiana* and the other is an orientation with the antero-dorsal part upward shown by *Lucinoma annulata, L. aokii,* and *Conchocele bisecta* (Fig. 16). It is notable that the latter three lucinaceans have a pointed anterior and tend to orient the anterior upward. In contrast, *A. stearnsiana* has a relatively rounded anterior and the antero-posterior axis is nearly horizontal.

Stanley (1970) described the life positions of seven lucinacean species: *Diplodonta notata, Codakia orbicularis, Phacoides pectinatus, P. muricatus, Anodontia alba* and *Lucina pensylvanica*. Excluding *D. notata* which shows an unusual upside-down life orientation, only *L. pensylvanica* assumes an orientation with its antero-dorsal part upward. In life position, the anterior mucus tube passes almost vertically upward, and the posterior siphon passes downward to discharge into the coarse sediment (fig. 34, Stanley, 1970). The remaining species, on the other hand, show a beak-up orientation, and discharge on the sediment surface. Stanley (1970) suggested that a pointed anterior of lucinacean shells indicates an anterior-up life position. The four examples described in this paper support Stanley's suggestion.

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地層中に保存された砂泥底生内生二枚貝化石の生息姿勢 —— 千葉県の第四系からの記載

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千葉県の第四系に産する砂泥底生内生二枚貝化石のうち，生息時の姿勢を保持していると考えられる19種について，それらの地層面に対する方向を計測した．また，一部の種については，これらの方向性と現生個体での観察結果との比較を行った．これらの多くは現生種であるが，ツキガイ超科やリュウグウハゴロモガイ科の二枚貝など，生息姿勢も含めてその生態があまり知られていない種が多い．地層中で観察された二枚貝化石の方向性は，同種の現生個体で観察された摂餌時の姿勢とほとんどの場合一致し，生息時の姿勢をよく保持していることが分かった．ただし，生息姿勢と異なり，しかも物理的に不安定な姿勢も少数観察された．

生息姿勢が保存されている二枚貝のほとんどは，深潜没生活者であるかまたは水流による攪乱の少ない内湾泥底の生息者である．このことは，例えば暴風時の海底侵食のような底質表面の物理的な攪乱が，浅潜没生活者や外洋種が生息位置で保存されることを妨げている主要な要因であることを示す．このほか，生物攪乱や埋没後の圧密も二枚貝化石の生息姿勢を死後変化させることがある．