divergent plication in bivalves can be achieved by excessive tangential growth of the mantle margin. However, the tablecloth wrinkle model suggests that in *M. ksakurai*, the excess mantle margin arose from a reduction in space resulting from mantle bending. McGhee (1978) investigated a hypothetical shell growth model and said that changes in whorl expansion rate and increment magnitude along the shell margin should produce irregularity along the commissure margin. In the case of *M. ksakurai*, the irregularity along the commissure margin was produced as a result of the collapse of the equilibrium between the whorl expansion rate and the shell secretion rate.

This study shows that the development and wide variation of plication in the shell of *M. ksakurai* are constrained mainly by an architectural factor (Bautechnischer Aspekt: Seilacher 1970; structural factor: Raup, 1972; "Can the machine be built?": Thomas, 1979; fabricational factor: Seilacher, 1991) derived from mantle bending. The bivalve shell is built as if by stacking of layers in the revolving commissure plane (Lison 1949; Raup and Michelson, 1965; Bayer 1978). Likewise, plication in *M. ksakurai* is created by stacking of layers in a distorted commissure plane.

It is important in constructing theoretical models of morphology to conceive of hard tissue construction in relation to mantle behavior (Savazzi, 1995). This paper proposes a plausible geometric model for plication formation in *Mytilus* (*Plicatomytilus*), without discussing physical properties of the mantle such as elasticity or viscosity. Study of these properties of the mantle during the growth of living bivalves will provide a reliable biophysical basis on which to consider the morphogenesis of molluscan hard tissues.

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Two Permian lyttoniid brachiopods from Akasaka, central Japan

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Abstract. Two lyttoniid brachiopod species, *Coscinophora magnifica* Cooper and Grant, 1974 and *Leptodus nobilis* (Waagen, 1883) are described from the Middle and Upper Permian limestones in the Akasaka district, Mino Belt, central Japan. The Permian brachiopod fauna of Akasaka is characterized by a mixture of both Tethyan and North American elements. The fauna is considered to have occupied a mid-equatorial region of the Panthalassa Ocean in Permian time.

Key words: Akasaka, brachiopods, central Japan, *Coscinophora magnifica, Leptodus nobilis*, Mino Belt, Permian

Introduction

The Akasaka district, northwest of Ogaki City in the Gifu Prefecture is a famous, classical area for the Japanese Permian. The Permian marine invertebrate fossils of the Akasaka Limestone in this district have been studied by many authors since the pioneering works of Schwager (1883), Gottsche (1884) and Ozawa (1927). Brachiopods from the Akasaka Limestone were studied by Sato (1919), Ozawa (1927) and Hayasaka (1925, 1932), and ten species were described or listed : *Lyttonia richthofeni* Keyser (Sato, 1919 ; Hayasaka, 1925 ; Ozawa, 1927), *Enteletes akasakensis* Ozawa (Ozawa, 1927 ; Hayasaka, 1932), *Scacchinella* cf. *gigantea* Gemmellaro (Hayasaka, 1925, 1932), *Reticularia lineata* Martin, *R. waageni* Loczy, *R.* cf. *inaequilateralis* Gemmellaro, *Terebratuloidea* ? sp. (Hayasaka, 1925), *Enteretes minoensis* Hayasaka, *E. suessi* Schellwien and *Geyerella* sp. (Hayasaka, 1932). Recently a lyttoniid species *Coscinophora magnifica* Cooper and Grant, from its lower part (*Parafusulina* Zone), was described and added to the list by Tazawa (1997b).

In this paper two lyttoniids from the Akasaka Limestone, *Coscinophora magnifica* Cooper and Grant, 1974 from its lower part (*Parafusulina* Zone) at Locality 1, Kinshozan, and *Leptodus nobilis* (Waagen, 1883) from its uppermost part (*Codonofusiella-Reichelina* Zone) at Locality 2, Hanaoka-yama, are described, and their palaeobiogeography is discussed. The fossil localities are shown on Figure 1. The first author (J.T.) is responsible for the systematic descriptions and discussion of Permian brachiopod palaeobiogeography, and the second and third authors (T.O. and M.H.) are responsible for field geology and collecting the specimens. All the specimens described here are stored in the Department of Geology, Faculty of Science, Niigata University.

Distribution of *Coscinophora* and *Leptodus*

The distribution of the genus *Coscinophora* is restricted stratigraphically and geographically. It has been described from only two regions, the Lower Permian (Wolfcampian) and Middle Permian (Leonardian) of west Texas, U.S.A. and the Middle Permian (*Parafusulina* Zone) of Akasaka, central Japan. *Coscinophora magnifica* Cooper and Grant has been known from the Middle Permian (Road Canyon Formation) of west Texas and the Middle Permian (lower part of the Akasaka Limestone) of Akasaka, central Japan (Sato, 1919 ; Hayasaka, 1925, 1932 ; Cooper and Grant, 1974 ; Tazawa, 1997b, this paper).

On the other hand, the genus *Leptodus* is widely distributed in the Lower to Upper Permian of the Tethyan and its neighboring regions. *Leptodus nobilis* (Waagen) is known from the Middle and Upper Permian of Hungary (Schréter, 1963), Croatia (Sremac, 1986), Serbia (Simic, 1933), Transcaucasia (Licharew, 1932 ; Sarytcheva, 1964 ; Ruzhentsev and Sarytcheva, 1965 ; Kotljar in Kotljar and Zakharov, 1989), Salt Range (Waagen, 1883 ; Noetling, 1904, 1905 ; Frech, 1911 ; Fredericks, 1916 ; Cooper and Grant, 1974) and Khisor Range (Grant, 1976) in Pakistan, Kumaon Himalayas (Diener, 1897), Kashmir (Diener, 1915), Cambodia (Mansuy, 1913, 1914 ; Termier and Termier, 1960 ; Chi-Thuan, 1961), Laos (Mansuy, 1912), Timor (Hamlet, 1928 ; Wanner and Sieverts, 1935), Port Keats in northern Australia (Thomas, 1957), Tibet (Zhan and

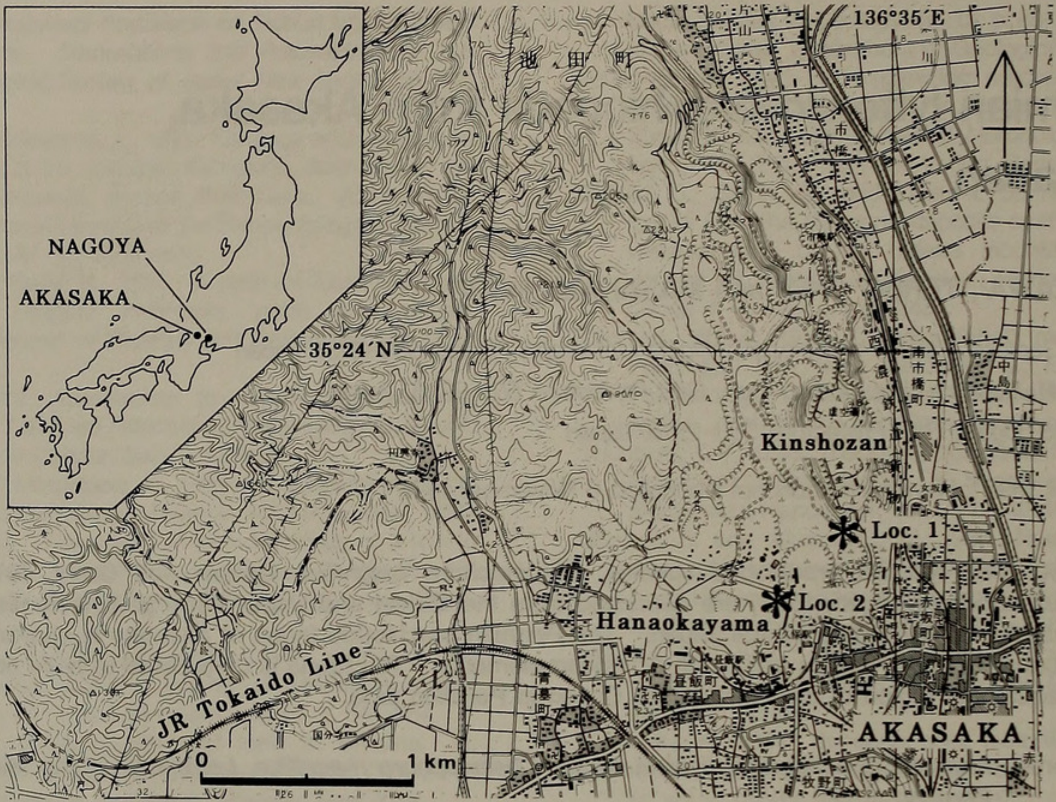

Figure 1. Map showing the fossil localities (using the topographical map of "Ogaki" scale 1 : 25,000 published by Geographical Survey of Japan).

Wu, 1982), Yunnan (Fang and Fan, 1994), Sichuan (Hayasaka, 1917, 1922b ; Huang, 1932), Guizhou (Hayasaka, 1917, 1922b ; Huang, 1932 ; Feng and Jiang, 1978), Guangxi (Huang, 1936 ; Yang *et al.*, 1977), Guangdong (Yang *et al.*, 1977 ; Zhan, 1979), Hunan (Yang *et al.*, 1977 ; Liao and Meng, 1986) and Hubei (Yang *et al.*, 1977 ; Yang, 1984) in South China, Jiangxi (Hayasaka, 1922b), Fujian (Wang *et al.*, 1982 ; Zhu, 1990) and Zhejiang (Liang, 1990) in East China, Gansu (Zhang *et al.*, 1983) and Qinghai (Jin *et al.*, 1979) in Northwest China, Inner Mongolia(Grabau, 1931 ; Lee and Gu, 1976 ; Lee *et al.*, 1980 ; Duan and Li, 1985 ; Gu and Zhu, 1985), Heilongjiang (Lee *et al.*, 1980) and Jilin (Lee *et al.*, 1980) in Northeast China, South Primorye in eastern Russia (Licharew and Kotljar, 1978), South Kitakami Belt (Yabe, 1900 ; Hayasaka, 1917, 1922a ; Tazawa, 1976, 1987 ; Minato *et al.*, 1979), Hida Gaien Belt (Tazawa, 1987 ; Tazawa and Matsumoto, 1998), Maizuru Belt (Mashiko, 1934 ; Shimizu, 1961) and Mino Belt (this paper) in Japan.

Permian reconstruction of the Akasaka Limestone

From the above data, it is clear that the genus *Leptodus* is a Tethyan element and the genus *Coscinophora* is a North American element, and the Permian brachiopod fauna of the Akasaka Limestone is a mix of Tethyan and North American elements.

The Akasaka Limestone is one of the limestone-greenstone blocks in the Jurassic melange of the Mino Belt in central Japan. The limestone-greenstone blocks are considered to have originated from reef-seamount complexes formed at the equatorial region of the Panthalassa Ocean in Permian time on the basis of palaeomagnetic (Hattori and Hirooka, 1977, 1979), sedimentological (Sano, 1988 ; Sano and Kanmera, 1996) and palaeontological data (Ishii *et al.*, 1985 ; Ozawa, 1987 ; Tazawa, 1991, 1992). However, none of these authors gave their opinion about the palaeolongitude of the Permian reef-sea mount complexes.

Tazawa (1997a, b) and Tazawa and Shen (1997) previously mentioned that these limestone-greenstone blocks were formed at the mid-equatorial region of Permian Panthalassa based on palaeobiogeographical studies of brachiopod faunas of the Hiyomo and Akasaka districts, Mino Belt. The occurrence of a typical Tethyan-type genus *Leptodus* together with a North American-type genus *Coscinophora* from the Akasaka Limestone strongly supports the above opinion.

Systematic descriptions

Order Productida Waagen, 1883
Suborder Strophalosiidina Waagen, 1883
Superfamily Lyttonioidea Waagen, 1883
Family Lyttoniidae Waagen, 1883
Subfamily Lyttoniinae Waagen, 1883
Genus ***Coscinophora*** Cooper and Stehli, 1955

Type species.—*Coscinophora nodosa* Cooper and Stehli, 1955

Coscinophora magnifica Cooper and Grant, 1974

Figures 2-3—5, 3

Coscinophora magnifica Cooper and Grant, 1974, p. 454, pl. 182, figs. 35, 36 ; pl. 184, figs. 1-8 ; pl. 185, figs. 1-17 ; pl. 186, figs. 1-13 ; pl. 187, figs. 1-11 ; pl. 188, figs. 15-22, 24 ; Tazawa, 1997b, p. 447, figs. 2-1—3.

Lyttonia richthofeni (Kayser). Sato, 1919, p. 276, text-fig. ; Hayasaka, 1932, p. 1.

Lyttonia sp. Hayasaka, 1925, p. 143, text-fig.

Material.—Three specimens, NU-B110-112, from the lower part (*Parafusulina* Zone) of the Akasaka Limestone at Locality 1, Kinshozan, Akasaka.

Description.—Shell large for genus, transversely subelliptical in outline ; length 56 mm, width 65 mm in the largest specimen (NU-B111). Pedicle valve slightly convex in lateral and anterior profiles except anterolateral margins which form steep slopes.

Pedicle valve interior with a median ridge and at least 12 lateral ridges, both of them consisting of a row of small beads. Lateral ridges rather regularly and symmetrically arranged on both sides of median ridge, nearly straight but slightly arched facing convexity towards front. Number and size of beads are obscure in the present material.

Brachial valve interior partly preserved in one specimen (NU-B110). Lateral lobes rather regularly and symmetrically arranged anteriorly on both sides of median lobe, but irregularly developed posteriorly. Each lateral lobe with a row of small, subrectangular holes, numbering 4 holes per 10 mm (Figure 3). Other internal structures not observed.

Remarks.—The present specimens are assigned to the genus *Coscinophora* on the basis of their pedicle valve moniliseptate, median and lateral ridges consisting of a row of beads, and their brachial valve median and lateral lobes consisting of a row of holes. These specimens are referred to *Coscinophora magnifica* Cooper and Grant, 1974, from the Road Canyon Formation of the Glass Mountains, west Texas, on account of the comparable size and shape of shell, and size and number of holes on the lateral lobes of the brachial valve.

The lyttoniid brachiopods collected from the lower part (Kasumi Zone of Wakimizu, 1902) of the Akasaka Limestone and reported as *Lyttonia richthofeni* (Kayser, 1883) (Sato, 1919, p. 276 ; Hayasaka, 1932, p. 1) and *Lyttonia* sp. (Hayasaka, 1925, p. 143) may be conspecific with the present species.

Genus ***Leptodus*** Kayser, 1883

Type species.—*Leptodus richthofeni* Kayser, 1883

Leptodus nobilis (Waagen, 1883)

Figures 2-1, 2-2, 4

Lyttonia nobilis Waagen, 1883, p. 398, pl. 29, figs. 1-3 ; pl. 30, figs. 1, 2, 5, 6, 8, 10, 11 ; Diener, 1897, p. 37, pl. 1, figs. 5-7 ;

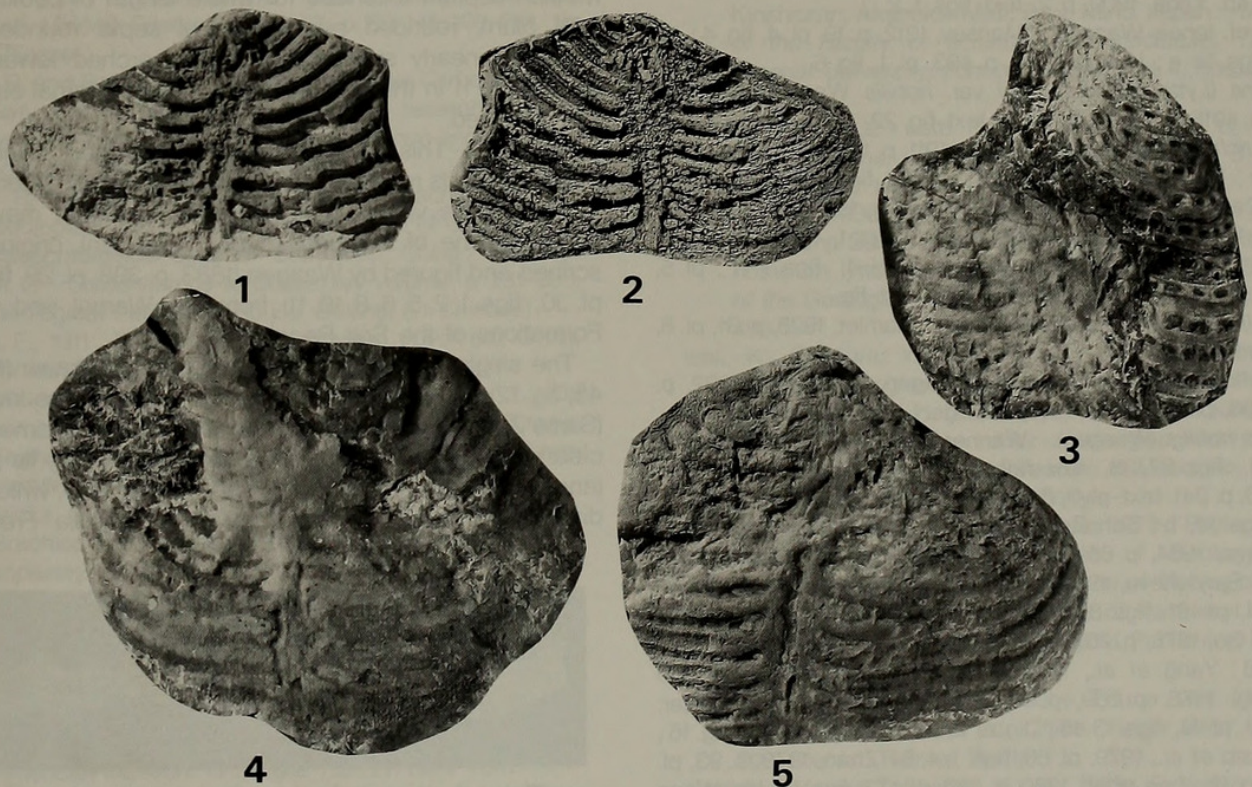

Figure 2. **1, 2.** *Leptodus nobilis* (Waagen, 1883). Internal mould of a pedicle valve and the latex cast, NU-B128. **3-5.** *Coscinophora magnifica* Cooper and Grant, 1974. Internal moulds of three pedicle valves, 3 : NU-B110 ; 4 : NU-B111 ; 5 : NU-B112. (All figures are natural size)

Figure 3. A part of the brachial valve of *Coscinophora magnifica* Cooper and Grant, 1974, showing details of the lateral lobes, NU-B110. (×3)

Noetling, 1904, p. 112, text-figs. 4-7 ; Noetling, 1905, p. 140, pl. 17, figs. 1, 2 ; pl. 18, figs. 1-11, text-fig. 2 ; Mansuy, 1913, p. 123, pl. 13, fig. 10 ; Mansuy, 1914, p. 32, pl. 6, figs. 7a-d ; pl. 7, figs. 1a-e ; Diener, 1915, p. 99, pl. 10, fig. 15 ; Grabau, 1931, p. 285, pl. 28, figs. 4, 5 only ; Huang, 1932, p. 89, pl. 7, figs. 9, 10 ; pl. 8, figs. 8, 9 ; pl. 9, figs. 1-8, text-figs. 8-11 ; Simic, 1933, p. 49, pl. 4, fig. 1.

Lyttonia tenuis Waagen, 1883, p. 401, pl. 30, figs. 3, 4, 7, 9.

Lyttonia sp. Yabe, 1900, p. 2, text-figs. 1, 2.

Lyttonia cf. *tenuis* Waagen. Mansuy, 1912, p. 19, pl. 4, fig. 4 ; pl. 5, figs. 1a-e ; Huang, 1936, p. 493, pl. 1, fig. 6.

Oldhamina (*Lyttonia*) *richthofeni* var. *nobilis* Waagen. Fredericks, 1916, p. 76, pl. 4, fig. 2, text-fig. 22.

Lyttonia richthofeni (Kayser). Frech, 1911, p. 135, pl. 20, figs. 2a, b only ; Hayasaka, 1917, p. 43, pl. 18, figs. 1-8 ; Hayasaka, 1922a, p. 62, pl. 11, figs. 1-6 ; Hayasaka, 1922b, p. 103, pl. 4, figs. 12, 13 ; Licharew, 1932, p. 56, 86, pl. 1, figs. 1-16 ; pl. 2, figs. 1, 2, 5, 7, 10, 12 ; pl. 3, figs. 2-7 ; pl. 4, figs. 1-17 ; pl. 5, figs. 1-4, 6 ; Mashiko, 1934, p. 182, text-fig.

Lyttonia (*Leptodus*) *richthofeni* Kayser. Hamlet, 1928, p. 31, pl. 6, figs. 1-4.

Lyttonia richthofeni forma *nobilis* Waagen. Licharew, 1932, p. 69, 96, pl. 2, figs. 13, 14 ; pl. 5, figs. 1-4, 6, text-fig. 3.

Leptodus nobilis (Waagen). Wanner and Sieverts, 1935, p. 249, pl. 9, figs. 27, 28, text-figs. 16-18 ; Termier and Termier, 1960, p. 241, text-pl. 3, figs. 1-10 ; Chi-Thuan, 1961, p. 274, pl. 1, figs. 1a, b ; Schréter, 1963, p. 107, pl. 3, figs. 5-8 ; Sarytcheva, 1964, p. 65, pl. 7, figs. 5-8, text-fig. 1 ; Ruzhentsev and Sarytcheva, 1965, pl. 39, figs. 6-8 ; Cooper and Grant, 1974, pl. 191, figs. 8, 9 ; Grant, 1976, pl. 43, figs. 18, 19 ; Lee and Gu, 1976, p. 267, pl. 162, figs. 1, 2 ; Tazawa, 1976, pl. 2, fig. 8 ; Yang *et al*., 1977, p. 371, pl. 147, fig. 5 ; Feng and Jiang, 1978, p. 269, pl. 100, fig. 2 ; Licharew and Kotljar, 1978, pl. 14, figs. 13-15 ; Jin *et al*., 1979, p. 82, pl. 23, fig. 15 ; Minato *et al*., 1979, pl. 66, figs. 1, 4, 5 : Zhan, 1979, p. 93, pl. 9, fig. 12 ; Lee *et al*., 1980, p. 389, pl. 172, figs. 15, 16 ; Wang *et al*., 1982, p. 229, pl. 95, fig. 20 ; Zhan and Wu, 1982, pl. 4, fig. 4 ; Zhang *et al*., 1983, p. 297, pl. 102, figs. 7, 8 ; Yang, 1984, p. 226, pl. 35, fig. 12 ; Gu and Zhu, 1985, pl. 1, figs. 31, 33, 34 ; Liao and Meng, 1986, p. 81, pl. 2, figs. 24, 25 ; Sremac, 1986, p. 30, pl. 10, figs. 1-2 ; Tazawa, 1987, fig. 1-11 ; Kotljar in Kotljar and Zakharov, 1989, pl. 20, fig. 6 ; pl. 23, fig. 12 ; Liang, 1990, p. 225, pl. 40, figs. 1, 5 ; Fang and Fan, 1994, p. 83, pl. 23, figs. 1-3 ; pl. 30, fig. 5 ; Tazawa and Matsumoto, 1998, p. 7, pl. 2, figs. 7-12.

Lyttonia cf. *nobilis* Waagen. Huang, 1936, p. 493, pl. 1, fig. 5.

Leptodus cf. *nobilis* (Waagen). Thomas, 1957, p. 177, pl. 20, figs. 1-6.

Leptodus richthofeni Kayser. Shimizu, 1961, pl. 18, figs. 14, 15 ; Schréter, 1963, p. 106, pl. 3, fig. 4 ; Sarytcheva, 1964, p. 65, pl. 7, figs. 2-4 ; Yang *et al*., 1977, p. 372, pl. 147, fig. 10 ; Yang, 1984, p. 226, pl. 35, fig. 11 ; Duan and Li, 1985, p. 119, pl. 35, figs. 17-19.

Leptodus ivanovi Fredericks. Minato *et al*., 1979, pl. 66, fig. 3.

Leptodus sp. Minato *et al*., 1979, pl. 66, fig. 2.

Leptodus tenuis (Waagen). Duan and Li, 1985, p. 119, pl. 35, figs. 14-16 ; Liang, 1990, p. 226, pl. 40, fig. 9 ; Zhu, 1990, p. 79, pl. 18, figs. 19-21 ; Fang and Fan, 1994, p. 83, pl. 23, figs. 4-5 ; pl. 30, fig. 6.

Leptodus sp. Tazawa, 1987, fig. 1-10.

Material.—One specimen, NU-B128, from the uppermost part (*Codonofusiella*-*Reichelina* Zone) of the Akasaka Limestone at Locality 2, Hanaokayama, Akasaka.

Description.—Shell medium to small for genus, transversely subtrigonal in outline, with flattened pedicle valve, having greatest width near anterior margin ; length 31 mm, width 53 mm.

Pedicle valve interior with regularly and symmetrically arranged lateral septa on both sides of median septum. Median septum extended for whole length of pedicle valve with blunt, rounded edge. Lateral septa rounded, solid (Figure 4), nearly straight, but slightly arched toward front, numbering 11 in the pedicle valve. Other internal structures not observed.

Remarks.—This specimen is safely assigned to the genus *Leptodus* by its rounded and solid (solidiseptate) lateral septa in the pedicle valve. The Akasaka specimen may be an immature one of *Leptodus nobilis* (Waagen), originally described and figured by Waagen (1883, p. 398, pl. 29, figs. 1-3 ; pl. 30, figs. 1, 2, 5, 6, 8, 10, 11) from the Wargal and Chhidru Formations of the Salt Range, Pakistan.

The single lyttoniid specimen figured by Ozawa (1927, pl. 45, fig. 12) as *Lyttonia richthofeni* Kayser from the lower part (Same Zone of Wakimizu, 1902) of the Akasaka Limestone is clearly distinguished from the present species by its grooved (angustilobate) lateral septa in the pedicle valve, which is the diagnostic character of the genus *Eolyttonia* Fredericks,

Figure 4. Longitudinal profile of the pedicle valve of *Leptodus nobilis* (Waagen, 1883). Right lateral view of a section of the latex cast, showing the lateral septa, NU-B128. (×2)

1924.

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