Guadalupian (Middle Permian) giant bivalve Alatoconchidae from a mid-Panthalassan paleo-atoll complex in Kyushu, Japan: A unique community associated with Tethyan fusulines and corals

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Abstract: Unique new fossil assemblages containing the large bivalve family Alatoconchidae are recorded from the Guadalupian (Middle Permian) shallow marine limestone in Kamura, Kyushu. The large bivalves occur in the *Neoschwagerina* Zone and *Lepidolina* Zone. This discovery establishes that the biostratigraphic range of the family Alatoconchidae extends up to the top of the *Lepidolina* Zone (upper Capitanian of upper Guadalupian) i.e., to the end-Guadalupian extinction level. The largest Alatoconchidae in Kamura occurs in the *Neoschwagerina* Zone, the size of which is up to 50 cm long and 5 cm thick. Although details are still unknown, their morphology with a wing-like side projection of their valves appears very similar to that of Alatoconchidae that includes the well-known genus *Shikamaia* Ozaki. The bivalve-bearing Iwato Formation was derived from a mid-oceanic shallow marine carbonate build-up formed on a mid-oceanic paleo-seamount. The close association among the Alatoconchidae, typical Tethyan fusulines (Verbeekinae) and rugose corals (Waagenophyllidae), plus their common extinction pattern suggests that the Alatoconchidae flourished in warm, shallow (photic) marine environments in low latitude areas in Panthalassa as well as Tethys. The extra-large size and double-layered shell with a translucent outer layer composed of prismatic calcite suggests that these bivalves may have hosted abundant photosynthetic algal symbionts to support their large-body metabolism.

Key words: Permian; bivalve; gigantism; seamount; Panthalassa; symbiosis.

Introduction. Aberration in shell size and morphology in bivalves has been reported from various periods of the Phanerozoic. Particularly noteworthy is the gigantism in bivalves with respect to symbiosis, as exemplified in Cretaceous rudists and in the modern bivalve genus *Tridacna*.¹⁾ In addition to rudists, ancient analogues of such giant clams include various taxa, such as Triassic megalodonts and Permian alatoconchids. The Permian bivalve family Alatoconchidae represents the oldest and largest example of such large-shelled bivalves of the Paleozoic, the shell of which may have reached 1 m in length.²⁾ Since the first description from Japan,³⁾ their occurrence has been reported from Cisuralian (Lower Permian) and Guadalupian (Middle Permian) rocks in several areas of

the world; i.e., Malaysia, Afghanistan, Iran, Croatia, and Tunisia.²⁾⁻⁸⁾ All of these except Japan were located in the low-latitude, warm-water realm of Tethys in Permian time, indicating the major distribution of this bizarre bivalve family.

The extraordinary shell morphology of Alatoconchidae has attracted great interest from paleontologists. Their unusual form with large wing-like folds on each valve suggests that they thrived in a reclining epifaunal life habit on a soft-sediment surface.²⁾ In addition, their double-layered shell with the external layer composed of prismatic calcite positively indicates that this bivalve family had photosynthetic symbionts. Despite their uniqueness in size and morphology, however, the first recognition of Alatoconchidae was relatively recent in the paleontological scene in the late 1960s, and the total number of fossil localities is still small, less than 10. Owing to the rarity in well-preserved

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Fig. 1. Index map of the Kamura area in Kyushu, southwest Japan (A, B), and the composite stratigraphic column of the study sections showing the horizons of Alatoconchidae (C). (B is modified from ref. 12. Note that almost identical Middle Permian limestones bearing Alatoconchidae occur in Akasaka and Neo in central Japan, ca. 500 km to the east. All three limestones likely formed not on a single but on different mutually-separated seamounts.

diagnostic specimens, the taxonomy of Alatoconchidae started with a considerable confusion, but Yancey and his colleagues^{2),9)} clarified the problem by proposing an overall model morphology and unique ligament structures as clear criteria for identification.

This article reports the first occurrence of a new large bivalve fauna composed of Alatoconchidae from central Kyushu, Japan, and discusses its geological significance with respect to the unique mid-oceanic, shallow marine facies developed in late Guadalupian mid-Panthalassa.

Geologic setting. The Middle Permian limestone at Kamura (Takachiho town, Miyazaki prefecture; Fig. 1a) in Kyushu forms part of an ancient mid-oceanic atoll complex primarily developed on a mid-oceanic paleo-seamount.¹⁰⁾ This limestone, like many other Permian limestones in Japan, occurs as an allochthonous block in

a Jurassic disorganized mudstone/sandstone of the Jurassic accretionary complex in the Chichibu belt. The limestone block at Kamura attains ca. 135 m in thickness and ranges in age from the Middle Permian to Late Triassic.¹¹⁾⁻¹⁵⁾ The Middle Permian Iwato Formation¹¹⁾ consists of a > 70 m-thick dark gray to black bioclastic limestone with a shallow marine fauna that includes fusulines, smaller foraminifera, bivalves, gastropods, brachiopods, rugose corals, and calcareous algae.¹⁵⁾ Fusulines are the most abundant, and provide a basis for dividing the Iwato Formation into 3 biostratigraphic units; i.e., the *Neoschwagerina* Zone, *Lepidolina* Zone, and a barren interval, in ascending order (unpublished data).^{10),11),15)} As the *Neoschwagerina* Zone and *Lepidolina* Zone contains abundant fusulines and calcareous algae, both intervals represent warm-water, shallow marine environments within the photic zone.

The Iwato Formation crops out in two sections in the Kamura area; i.e., Sections 1 and 2 (Fig. 1b, c). Large bivalves occur in most parts of the Iwato Formation, and highly concentrated parts are exposed in the *Neoschwagerina* Zone of Section 1 (southeast of Saraito village; 32°45'12"N, 131°20'55"E) and in the *Lepidolina* Zone of Section 2 (south of Shioinouso; 32°44'58"N, 131°20'02"E). Detailed stratigraphy of Section 1 will be described elsewhere, and the *Neoschwagerina*-bearing interval is here tentatively called the *Neoschwagerina* Zone. See Ota & Isozaki¹⁵⁾ for the detailed lithostratigraphy and fusuline biostratigraphy of the upper part of the Iwato Formation at Section 2 that includes the *Lepidolina* Zone.

Large bivalve shells occur in a ca. 5 m-thick argillaceous limestone in the lower part of Section 1. Bivalve shells are concentrated to form coquina beds, showing a preferred bedding-parallel alignment (Fig. 2a). This horizon yields many large shells including the largest from the Kamura area (Fig. 2b) but this bivalve assemblage is monotonous and low in diversity. The host limestone is composed of black lime mudstone with matrix-supported bioclasts, such as fragments of bivalve shells, gastropods, brachiopods, fusulines, smaller foraminifera, and calcareous algae (Dasycladaceans). Identified fusulines include *Neoschwagerina* sp. and *Verbeekina* sp. This zone is correlated with the lower Maokouan in South China, the Murgabian in Transcaucasia, and the Wordian of the Guadalupian in Texas.

At Section 2, the bivalve shells, much smaller than those at Section 1, occur in a > 6 m-thick black to dark gray limestone in the lower part of the section that was described as the *Lepidolina* Zone.¹⁵⁾ Shells are concentrated in several horizons to form coquina beds intercalated between fusuline-dominant parts (Fig. 2e, f). Diversity is low both in fusulines and bivalves. The host limestone is composed of black wackestone with bioclasts dominated by abundant fusulines with a minor amount of smaller foraminifera, bivalves, gastropods, and calcareous algae (Dasycladaceans). Identified fusulines include *Lepidolina* cf. *shiraiwensis* (Ozawa), *Colania* sp., and *Khalerina* sp. This zone is correlated with the upper Maokouan in South China, the Midian in Transcaucasia, and the upper Capitanian of the Guadalupian in Texas.

Large bivalves. As most of the bivalve shells are tightly connected to the matrix, it is difficult to isolate free individual specimens. Thus observation is limited to sections of shells on surface exposures and on randomly

sliced rock slabs. Although almost all shells are broken in part and not intact as in their living position, an average dimension of shell is estimated by measuring the apparent length and thickness on the surface sections.

The shell sizes of the bivalves of the *Neoschwagerina* Zone vary considerably; most are ca. 30 cm long and 10–30 mm thick (Fig. 2a). Shells are mostly planar to gently curved. The largest valve, partly broken, reaches ca. 50 cm in length and 50 mm in thickness (Fig. 2b), suggesting that the complete shell was much larger. The most unique characteristic of these shells is a tight isoclinal fold observed in section (Fig. 2c, d). In general, the axial parts of the U-shaped fold tend to be thicker than the rest. The insides of the shells are filled with black argillaceous lime mudstone that is similar to that of the surrounding matrix. Hinge and ligament parts, as well as inner shell ornamentations, cannot be clearly observed.

In contrast, in the *Lepidolina* Zone, the shell sizes of the bivalves are much smaller; less than 30 cm long and less than 10 mm thick (Fig. 2e, f). The shells are mostly planar to gently curved, and tight isoclinal folds with U-shaped corner are often observed in section (Fig. 2f). Despite their smaller size, these shells in the *Lepidolina* Zone are by and large identical to those in the *Neoschwagerina* Zone in having a unique isoclinal fold and in their mode of occurrence. No well-preserved hinge/ligament part of valves or inner shell ornamentations has been recognized.

Microscopic observation reveals that the shells of the large bivalves from the two horizons have a unique double-layered structure (Fig. 2f, g). The external layer is composed of long prismatic calcite aligned perpendicular to the shell surface, whereas the internal layer consists of microgranular mosaic calcite (Fig. 2h). Each prismatic calcite in the external layer is mostly 1 to 5 mm long and 100 micrometer in diameter (Fig. 2i); the longest (in the *Neoschwagerina* Zone) reaches ca. 1 cm (Fig. 2j).

The taxonomic position of the large bivalves from the Kamura area is not precisely determined at present because no complete free specimen, with a well-preserved hinge and ligament structure of valves or inner shell ornamentations, has so far been obtained. Nonetheless, their extraordinarily large size, the wing-like fold of their valves, and their Middle Permian age suggest that these large bivalves belong to the family Alatoconchidae. This family was established for Middle Permian specimens from Afghanistan.⁵⁾ On summarizing additional material from Malaysia, Tunisia, and Croatia,

Fig. 2. Alatoconchidae gen. et sp. indet. from the Kamura area and their shell structure. a: large shell bed in Section 1 (*Neoschwagerina* Zone), b: the largest shell is over 50 cm long (enlarged part of a), c, d: characteristic U-shaped isoclinal fold in valve (Section 1), e: shell bed in Section 2 (*Lepidolina* Zone), f: polished slab of a shell bed (e) showing the double-layered shell (ext.: external layer; int.: internal layer), g-i: photomicrographs of double-layered shell of Alatoconchidae from Section 2 (g, h: layer-normal section of the external layer, i: layer-parallel section), j: photomicrographs of the external layer of Alatoconchidae from Section 1 (layer-normal section). Note the layer-normal aligned prismatic calcites (1-5 mm long, 0.1-0.2 mm in diameter) forming the external layer (g-i) and very long (ca. 8 mm) prismatic calcite, in the external layer of a shell from Section 1 (j).

Yancey & Boyd²⁾ later re-defined the family as “large to very large equivalved shells with elongate or circular outline in dorsal view; shell wall thick, with massive infilling of umbonal cavity, but thin on leading edge; beaks commonly terminal; umbonal carina alate, compressed dorsoventrally and laterally produced, resulting in distinctive wing-like flanges formed by reflexed valve wall; very large flat ventral surface, bounded by umbonal carina; ligament duplivincular; byssal groove present, but non-functional in adults of some species; outer shell layer composed of very large simple prisms set perpendicular to shell surface”. This family includes two genera; i.e. *Shikamaia* Ozaki (with three subgenera, *Shikamaia* s.s. Ozaki, *Tanchintongia* Runnegar & Gobbett, and *Alatoconcha* Termier, Termier & Lapparant) and *Saikraconcha* Yancey & Boyd (with two subgenera, *Saikraconcha* s.s. Yancey & Boyd and *Dereconcha* Yancey & Boyd). *Shikamaia akasakaensis* Ozaki represents the first recognized taxon of this family, which was originally described from the Akasaka limestone in central Japan (Fig. 1a).³⁾ Its morphology was so bizarre that the genus *Shikamaia* was not initially identified even as a bivalve, however, this genus was later incorporated into the family Alatoconchidae.^{2),9)}

The geologic setting of Alatoconchidae from Kamura is identical with that of *Shikamaia akasakaensis* Ozaki from Akasaka.^{3),9)} The Permian limestone in Kamura is tightly correlated with the Akasaka limestone.¹⁵⁾ This correlation positively indicates that the present material from Kamura is probably comparable with the genus *Shikamaia* from Akasaka. However, it is still difficult to identify it at a genus level solely on the basis of current observations on sections. Therefore, all the large bivalves from the *Neoschwagerina* Zone and *Lepidolina* Zone in Kamura are here treated as Alatoconchidae gen. et sp. indet.

The co-occurrence of Dasycladacean algae indicates that the water-depth of their habitat was within the photic zone, less than 50 m deep.¹⁵⁾ Most of the shells are partly broken, probably due to the fragile shell structure with a remarkably large contrast between size and thickness. However, some shells show a preferred upward-concave alignment, indicating that they are nearly in their living position, i.e., reclining on a mud-dominant soft substrate using a unique flat bottom surface like a snowshoe.²⁾

Discussion. The giant clams Alatoconchidae with a length of more than 50 cm occur in the *Neoschwagerina* Zone in Kamura. The

Neoschwagerina Zone is correlated with the middle-upper Murgabian in Transcaucasia, and with Wordian (Middle Guadalupian) in Texas. The occurrence of the family Alatoconchidae in the world is restricted to Lower to Middle Permian rocks, and there is none reported from the Upper Permian. Concerning the Middle Permian examples, the holotype of *Shikamaia akasakaensis* Ozaki was reported in the *Parafusulina* Zone in the Akasaka area³⁾ (Fig. 1a) together with a very large incomplete specimen probably reaching 1 m in full length. There are further reports of the occurrence of Alatoconchidae in the *Neoschwagerina* Zone in Croatia⁷⁾ and in Tunisia.⁸⁾ The large specimens ever reported of *S. akasakaensis* Ozaki, up to 90 cm in length, occur in the Neo area in Japan, ca. 30 km to the north of the Akasaka area (Fig. 1a).⁹⁾ The relevant horizon was originally described as in the *Neoschwagerina* Zone, but was later amended as in the *Pseudofusulina ambigua* Zone of upper Cisuralian,¹⁶⁾ indicating that the family Alatoconchidae likely attained its dominance and maximum size in the late Early Permian, and extended its lineage into the Middle Permian.

Although the shell size became smaller, noteworthy is the abundant occurrence of smaller Alatoconchidae in the *Lepidolina* Zone in Kamura (Figs. 1c, 2e, f). The *Lepidolina* Zone is correlated with the Midian in Transcaucasia and with the upper Capitanian (upper Guadalupian). This newly recognized horizon marks the highest horizon of Alatoconchidae hitherto reported. Similar large bivalves also occur in the *Yabeina* Zone (correlated with the Capitanian) in Akasaka.¹⁵⁾ By forming several remarkable coquina beds, Alatoconchidae occur abundantly in Kamura, but they disappeared sharply at the top of the *Lepidolina* Zone together with large-shelled fusulines and never returned in higher horizons.¹⁵⁾ In other words, the Alatoconchidae were terminated abruptly in the end-Guadalupian extinction event like many other marine invertebrate taxa.¹⁷⁾⁻¹⁹⁾

The Permian limestone in Kamura was derived from an ancient atoll-type carbonate buildup developed on a paleo-seamount in low-latitude mid-Panthalassa.^{10),15)} The occurrence of Alatoconchidae in Kamura indicates that this bizarre bivalve family thrived in a shallow marine environment on a seamount in the Middle Permian superocean. The good equivalent of the Alatoconchidae-bearing Guadalupian limestone in Akasaka^{3),9)} is at present physiographically separated by more than 500 km from the Kamura area (Fig. 1a), and this separation suggests that the Akasaka and Kamura

Fig. 3. Late Permian paleogeographic map²³⁾ showing the occurrence of large bivalve Alatoconchidae, i.e., Japan, Malaysia, Afghanistan, Iran, Croatia, and Tunisia (compiled from 3-9). Open circle: Guadalupian (Middle Permian), open square: Cisurarian (Lower Permian). Note their distribution concentrated in the low latitude Tethyan domain, except for mid-Panthalassan paleo-atoll complexes currently exposed in Kamura, Akasaka and Neo in Japan (open star).

limestones formed on different seamount complexes.¹⁰⁾ Nevertheless, it is noteworthy that these two limestones share almost the same tectono-sedimentary origin in the mid-superocean, and have the same lithofacies mostly composed of black to dark gray massive limestone (lime mudstone and wackestone) with a relatively high organic carbon content. Their fine-grain size without any water-agitation features suggests deposition in a lagoon facies in a carbonate build-up. The uniformity between the two limestones positively indicates that this facies may have represented one of the regional environments in Guadalupian shallow mid-Panthalassa. This unique Guadalupian facies often recognized in accreted paleo-atoll complexes in SW Japan was named the Kinshozan facies.²⁰⁾ Nearly a half century ago, Hayasaka & Hayasaka²¹⁾ already pointed out the peculiarity of the large-sized bivalves and gastropods of Akasaka, and suggested that the large mollusks may have been adapted to a unique bituminous facies. The Alatoconchidae-bearing Lower Permian limestone in the Neo area also shares the same facies.¹⁶⁾ Thus the Alatoconchidae likely preferred such a lagoon facies on ancient seamounts in low-latitude mid-Panthalassa. The latest analysis of stable carbon isotope ratios²²⁾ indicates that the *Lepidolina* Zone (immediately before the disappearance of the Kinshozan facies) in Kamura corresponds to a period of unusually high bio-productivity

even in an oligotrophic environment like a mid-oceanic atoll.

Except for the above-mentioned three examples of mid-oceanic habitat, other occurrences of Alatoconchidae are limited strictly to circum-Tethyan shelf domains; i.e., Tunisia, Croatia, Iran, Afghanistan, and Malaysia (Fig. 3).⁴⁾⁻⁸⁾ However, the giant bivalves occur not necessarily throughout the whole of Tethys, as there is no report from South China despite its fossiliferous nature in general. Nonetheless, it is clear that Alatoconchidae was absent in the marine Permian in high-latitude areas, such as Greenland/Spitsbergen and Australia. This further supports the adaptation of Alatoconchidae to a low-latitude, warm-water environment that spanned across Tethys and low-latitude Panthalassa.

Alatoconchidae is almost always associated closely with the fusuline family Verbeekinae and rugose coral family Waagenophyllidae.⁹⁾ Such an association is typically observed in the Akasaka limestone. In Kamura, Verbeekinae occurs abundantly, whereas Waagenophyllidae is present but rare.¹⁵⁾ The last two families are well-known representatives of the Tethyan assemblage of the Middle Permian. Thus Alatoconchidae, as well as the Tethyan large-shelled fusulines and rugose corals, was probably adapted to such a shallow, warm-water environment that developed

over the middle of the superocean in a low latitude, although constrained to the top parts of paleo-seamount chains. These Tethyan invertebrates probably migrated in their planktonic larval stage into mid-Panthalassa along the equatorial seamount chain.

In general, the fact that mollusks keep an extraordinarily large body requires an extremely high cost for their metabolism coupled with sufficient nutrient supply. As is observed in modern *Tridacna* and Cretaceous rudists, symbiosis with various photo- or chemo-autotrophs is regarded as the most promising and the most commonly-used strategy for various large-size taxa particularly in oligotrophic environments.^{1),24),25)} Accordingly, an extraordinarily large size and a bizarre morphology of bivalves are often regarded as indications of symbiosis; however, this is generally difficult to prove if ancient analogues performed symbiosis solely on the basis of their shell morphology. In this regard, noteworthy is the double-layered shell structure of Alatoconchidae, in particular, the external layer composed of large prismatic calcites. From microscopic observation of the shell structure of Alatoconchidae, Yancey & Boyd²⁾ concluded that these bivalves probably hosted photosynthetic algal symbionts.

The present observations confirm precisely the same double-layered shell structure of Alatoconchidae from both the *Neoschwagerina* and *Lepidolina* Zones (Fig. 2f-h). In the external layer of the shells, large calcite prisms, 1-10 mm in length, are systematically aligned perpendicular to the shell surface (Fig. 2g, h). Like optical fibers, large elongated crystals without growth surfaces can easily conduct sunlight into a bivalve's interior, where abundant photosynthetic symbiont algae are accommodated within a bivalve's mantle, as observed in the modern bivalve genus *Corculum*.¹⁾ Thus the Alatoconchidae in Kamura is regarded to have hosted photosynthetic symbiont algae.

The bioclasts associated with Alatoconchidae include abundant fusulines with minor rugose corals, calcareous algae (Dasycladaceans), and crinoids, suggesting that the Permian limestone in Kamura was deposited in the photic zone.¹⁵⁾ In addition, they are associated with the large-shelled Verbeekinae fusulines that are supposed to have had photosynthetic algal and/or cyanobacterial symbionts.^{15),26),27)} Rugose corals likewise hosted algal symbionts. Thus the Guadalupian community composed of the trio (Alatoconchidae, Verbeekinae, and Waagenophyllidae) may have been considerably symbiosis-dependent, and represents a unique niche in the low-latitude, shallow mid-ocean.

Modern large photosymbiotic bivalves are ecological *K*-strategists restricted solely to tropical reef and pelagic environments,²⁴⁾ which is consistent with the depositional site of the Permian giant clam-bearing limestone.

This interpretation is in good accordance with the pattern of synchronous extinction or diversity decline in Alatoconchidae and Verbeekinae, as well as of Waagenophyllidae. The disappearance of the first two was very sharp at the top of the *Lepidolina* Zone in Kamura (and the *Yabeina* Zone in Akasaka)¹⁵⁾ and they never returned in higher horizons. The symbiosis-dependent fauna, probably much too adapted to the temporally stable condition on seamounts, may have been terminated when a rapid change appeared at the end of the Guadalupian. Stable carbon isotope data from Kamura suggest that a remarkable cooling occurred in the Capitanian.²²⁾ Symbiotic organisms adapted to the warm-water environment, such as the trio of Alatoconchidae-Verbeekinae-Waagenophyllidae may have become particularly vulnerable for extinction during this cooling period.

In summary, new large bivalve Alatoconchidae gen. et sp. indet. are reported from the Guadalupian limestone derived from a mid-oceanic paleo-atoll complex in Kyushu, Japan. This find extends the stratigraphic range of the family Alatoconchidae up to the *Lepidolina* Zone (upper Capitanian, Upper Guadalupian), and expands its paleogeographical distribution to a much wider area than previously regarded. A double-layered shell structure strongly supports the idea that these giant clams performed symbiosis with photosynthetic algae in shallow-water (photic zone) on a seamount in the middle of the superocean. More detailed paleontological work is definitely required of these newly discovered unique large bivalves.

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