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Morphology, systematics and paleoecology of *Shikamaia*, aberrant Permian bivalves (Alatoconchidae: Ambonychioidea) from Japan

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Abstract. The extraordinarily large and aberrantly shaped shells of the Permian bivalve family Alatoconchidae (Ambonychioidea), thought to have a photosymbiotic mode of life like the modern fragine bivalve *Corculum*, are difficult to extract from their host limestone bodies; therefore, their morphologies have been reconstructed mostly based on broken shell pieces. The alatoconchid *Shikamaia akasakaensis* Ozaki, the type species of the genus from the middle Permian Akasaka Limestone of central Japan, was described based on only three fragmentary specimens; its shell characters were later reassessed from specimens from the Neo area, *ca.* 30 km NNE of the type locality. Because of the fragmentary nature of the type specimens of *S. akasakaensis*, this species is difficult to diagnose and cannot be compared taxonomically to the specimens from the Neo area or other known species. A shell reconstruction based on 19 specimens from the type locality shows that *S. akasakaensis* exhibits a very large, elongated elliptical shell form but clearly differs from the Neo specimens in its higher and longer dorsal crests and more dorsally reflected shell wings in the anterior portion, rendering the establishment of a new species (*Shikamaia ozakii* Asato and Kase sp. nov.) for the latter specimens. The outer shell consists of a very thin outermost prismatic layer that is underlain by thick layers of granular crystals in both species of *Shikamaia*, which suggests that the shell did not allow sufficient sunlight penetration to culture symbiotic microbes in the soft tissues of these animals. The "*Corculum* model" of photosymbiosis therefore is unlikely for the two species of *Shikamaia*. The discovery of the presence of a ventral gape, a previously unreported shell character, suggests extension of the soft body into the sediment through this opening during life. Three possible modes of life (fragine-like photosymbiosis, lucinid-like chemosymbiosis and normal suspension feeding) are discussed.

Key words: Akasaka Limestone, Alatoconchidae, Bivalvia, Permian, *Shikamaia*, taxonomy

Introduction

Members of the family Alatoconchidae Termier *et al.*, 1973 are among the largest Permian bivalves (occasionally reaching an antero-posterior length of over 1 m), have a dorso-ventrally compressed shell form (alatoform) like the modern cardiid bivalve *Corculum cardissa* Linnaeus, 1758, and are thought to belong to the superfamily Ambonychioidea Miller, 1877. To date, this family accommodates four genus/subgenus taxa (*Shikamaia* Ozaki, 1968; *Alatoconcha* Termier *et al.*, 1973; *Saikraconcha* Yancey and Boyd, 1983; *Dereconcha* Yancey and Boyd, 1983) and six species (Yancey and Boyd, 1983), and has been reported from the lower and middle Permian (upper Cisuralian to Guadalupian) shallow marine carbonates in nine widely separated areas (Croatia, Tunisia, Oman, Afghanistan, Iran, Thailand, Malaysia, the Philippines and Japan) once located at low latitudes of the Panthalassa and Tethyan seas (Ozaki, 1968; Termier *et al*., 1973; Runnegar and Gobbett, 1975; Yancey and Ozaki, 1986; Kochansky-Devidé, 1978; Boyd and Newell, 1979; Thiele and Tichy, 1980; Kiessling and Flügel, 2000; Isozaki, 2006; Udchachon *et al*., 2007; Aljinović *et al*., 2008; Isozaki and Aljinović, 2009). Alatoconchids attained their largest shell size in the Wordian (middle Guadalupian) and became extinct either during the Capitanian (late Guadalupian) cooling Kamura event or around the Guadalupian-Lopingian boundary (Isozaki, 2006; Ota and Isozaki, 2006; Udchachon *et al*., 2007; Aljinović *et al*., 2008; Isozaki and Aljinović, 2009; Kofukuda *et al*.,

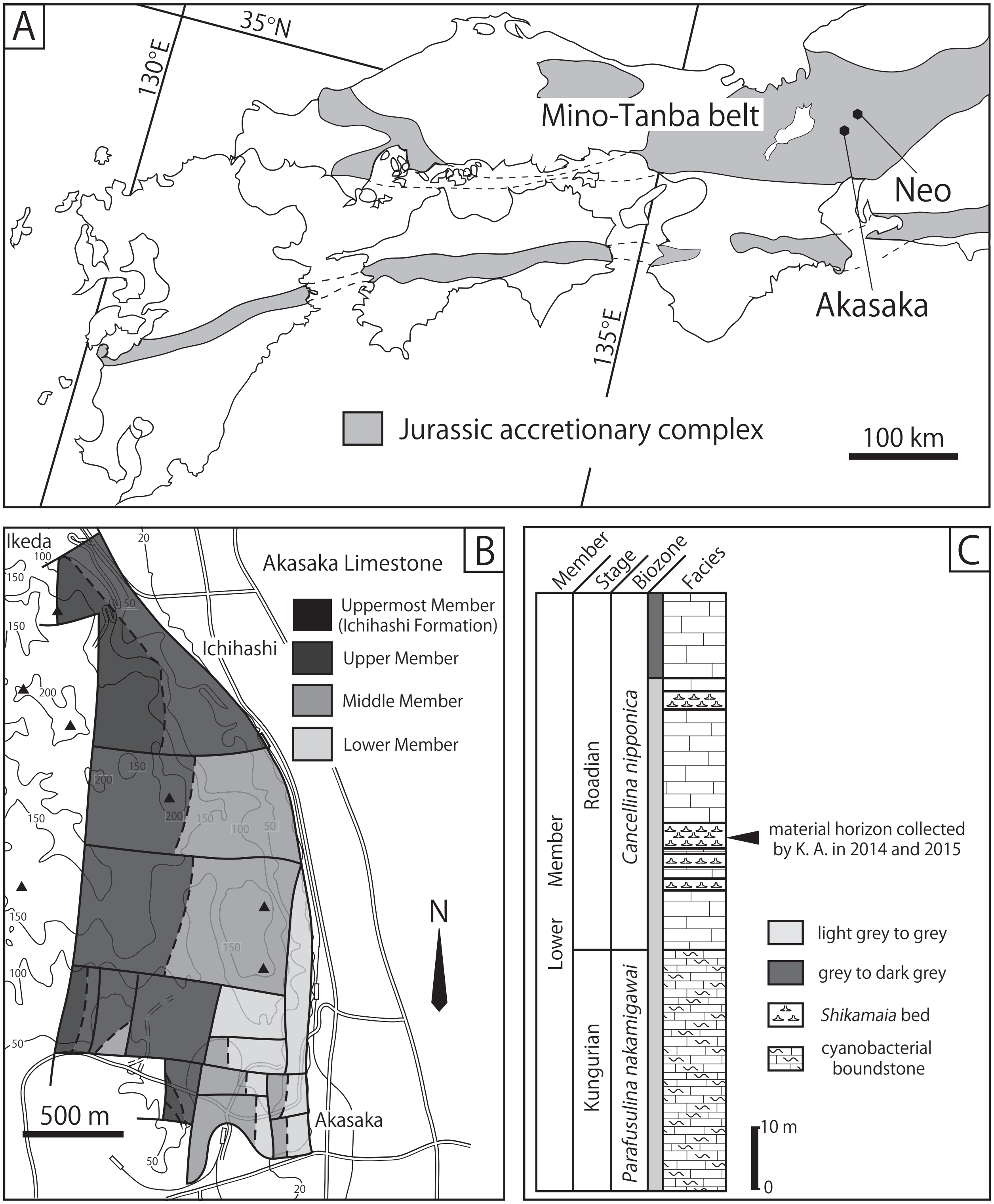

Figure 1. **A,** location map of the Akasaka and Neo areas within the Mino-Tanba belt, modified after Ota and Isozaki (2006); **B,** geological sketch map of the Akasaka Limestone, modified after Ota and Isozaki (2006) and Kobayashi (2011); **C,** stratigraphic column of the Lower Member of the Akasaka Limestone. The column is modified after Kobayashi (2011). Arrow indicates the bed in which the first author collected the sample used mostly in this study.

2014; Udchachon *et al*., 2014). They usually occur in aggregation to form 'alatoconchid beds' (Runnegar and Gobbett, 1975; Sano, 1988; Ozawa and Nishiwaki, 1992; Isozaki, 2006; Ota and Isozaki, 2006; Udchachon *et al*., 2007; Aljinović *et al*., 2008; Isozaki and Aljinović, 2009; Kobayashi, 2011; Nishiwaki *et al*., 2011, 2013; Kofukuda *et al*., 2014; Udchachon *et al*., 2014). However, because of severe recrystallization and deformation/breakage by sediment compaction, the collection and preparation of whole shells is difficult.

Shikamaia akasakaensis Ozaki, 1968, originally regarded as Animalia incerta sedis, was the first named alatoconchid and occurs from the middle Permian Akasaka Limestone in a still actively operating limestone quarry on Mt. Kinshozan in the Akasaka area of Ogaki City, Gifu Prefecture, central Japan (Figure 1). The Akasaka Limestone is an allochthonous limestone body within the Mino-Tanba Belt, a Jurassic accretionary complex in Southwest Japan (Ozawa and Nishiwaki, 1992; Isozaki, 1997; Isozaki and Ota, 2001; Ota and Isozaki, 2006; Asato *et al.*, 2016) and originated on a low-latitude paleo-atoll in the Panthalassan Ocean (Ozawa and Nishiwaki, 1992; Zaw Win, 1999, 2000; Ota and Isozaki, 2006; Kasuya *et al*., 2012; Isozaki, 2014; Isozaki and Kase, 2014; Kirschvink *et al.*, 2015). Like other alatoconchids, *S. akasakaensis* was described based on a small number of fragmentary specimens that do not provide sufficient information on the whole shell outline and the ligamental characters important for the suprageneric taxonomy. Yancey and Ozaki (1986) later clarified the umbonal and ligamental characters of this species based on the umbonal portion of an articulated valve pair from the middle Permian Funabuseyama Formation in the Neo area, another allochthonous limestone body in the Mino-Tanba terrane, about 30 km NNE of the Akasaka area. However, it remains uncertain whether the specimens from the Akasaka and Neo areas belong to the same species. Light-colored alatoconchid shells exhibit unique and often artistic sectional patterns on typically dark-colored, eroded limestone surfaces. Because these taxa are easily recognizable in outcrops, additional occurrences of alatoconchids have been found in Japan by both professional (Isozaki, 2006) and amateur paleontologists since their description by Ozaki (1968). In particular, the occurrences of at least two additional forms of alatoconchid in the Akasaka Limestone and Permian limestone bodies in other areas of Japan suggest that alatoconchids on the Japanese Archipelago are more diverse than previously thought (Kubo, 2012, 2013; Asato *et al.*, 2015).

The focus of this study is to elucidate the whole shell morphology of *Shikamaia akasakaensis* based on materials from the Akasaka Limestone and the Funabuseyama Formation, and to investigate the affinity between specimens from the Akasaka and Neo areas as well as with other previously described species.

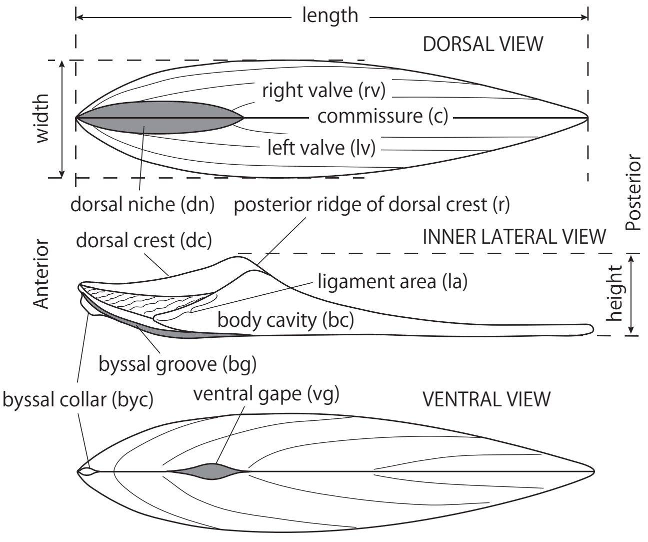

Figure 2. Terminology, orientation and measurements in *Shikamaia*.

All examined specimens herein are deposited in the Invertebrate Paleontology collection in the Department of Geology and Paleontology, the National Museum of Nature and Science, Tsukuba, Japan with prefix NMNS. Shell orientation and terminology follow those defined by Yancey and Boyd (1983) for *Shikamaia perakensis*, as well as those defined by Posenato *et al*. (2013) for the Jurassic alatoform bivalve *Opisoma excavatum* (Boehm, 1884) (Figure 2).

Material

We examined *Shikamaia akasakaensis*-bearing wackestone blocks obtained by K. A. in 2015 and 2016 and those collected by T. K. in the late 1980s, all from the Lower Member of the Akasaka Limestone (Figure 1B). Kobayashi (2011) recognized four *Shikamaia*-bearing beds in the Lower Member (Figure 1C). Because the limestone quarry at Mt. Kinshozan has been extensively operated, the collecting sites of Ozaki (1968) and T. K. were already quarried out, and the present exposure of the *Shikamaia*-bearing beds may have moved backward for a substantial distance over the last 50 years. Therefore, the collecting sites of the specimens studied by Ozaki (1968) and those examined in this study are not exactly the same. Ozaki (1968) wrote that he obtained his material from the 'Kasumi Limestone', which belongs to the *Parafusulina* Zone *sensu* Akasaka Research Group (1956). The 'Kasumi Limestone' defined by Wakimizu

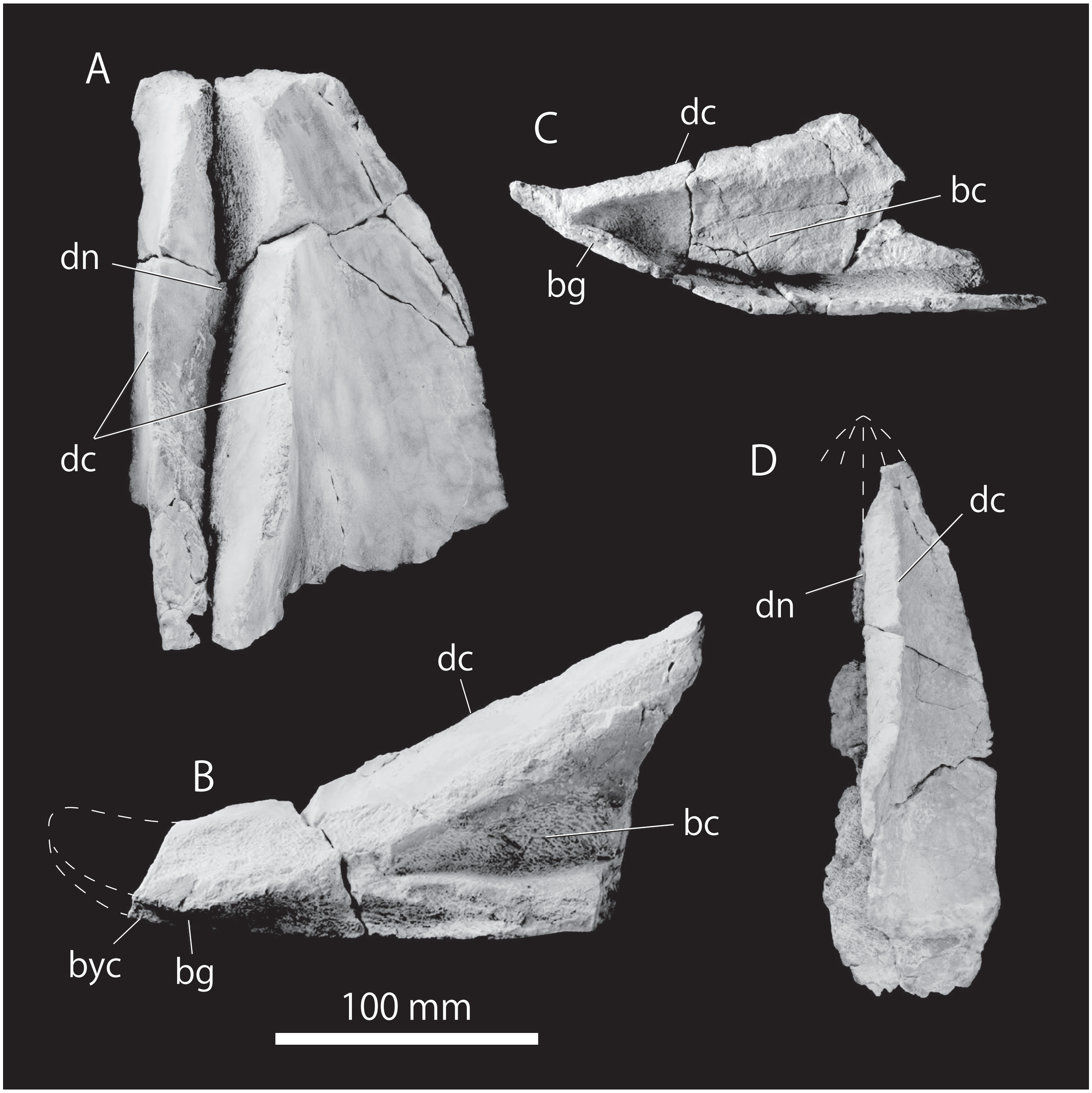

Figure 3. *Shikamaia akasakaensis* Ozaki, 1968 from the middle Permian Akasaka Limestone. **A, B,** NMNS PM27546; A, dorsal view of a fragmentary articulated shell, showing the well developed dorsal niche (dn); B, inner lateral view of the left valve, showing the byssal grooves (bg) and the byssal collar (byc); **C, D,** NMNS PM27559, dorsal (C) and inner lateral (D) views of a small right valve, showing the anterior part of the dorsal niche (dn), dorsal crest (dc) and body cavity (bc). Byssal collar is missing in this specimen.

(1902) is equivalent to the *Shikamaia*-bearing light-gray wackestone/packstone in the Lower Member of the Akasaka Limestone (Kobayashi, 2011). Therefore, all the specimens examined in this paper come from the Roadian light-gray wackestone/packstone beds of the Lower Member. The specimens collected by K. A. are probably from the third bed from the bottom of the *Cancellina nipponica* Zone by Kobayashi (2011), but the precise horizons of the specimens of Ozaki (1968) and collected by T. K. are unknown. Based on our observations of the cross-sectional aspect exposed on the limestone surfaces, it is likely that the shells from the Lower Member belong to a single species, *S. akasakaensis*.

The Neo specimens occur in black wackestone/packstone beds of the Funabuseyama Formation [= Tokuyama Formation of Yancey and Ozaki (1986)] exposed in the

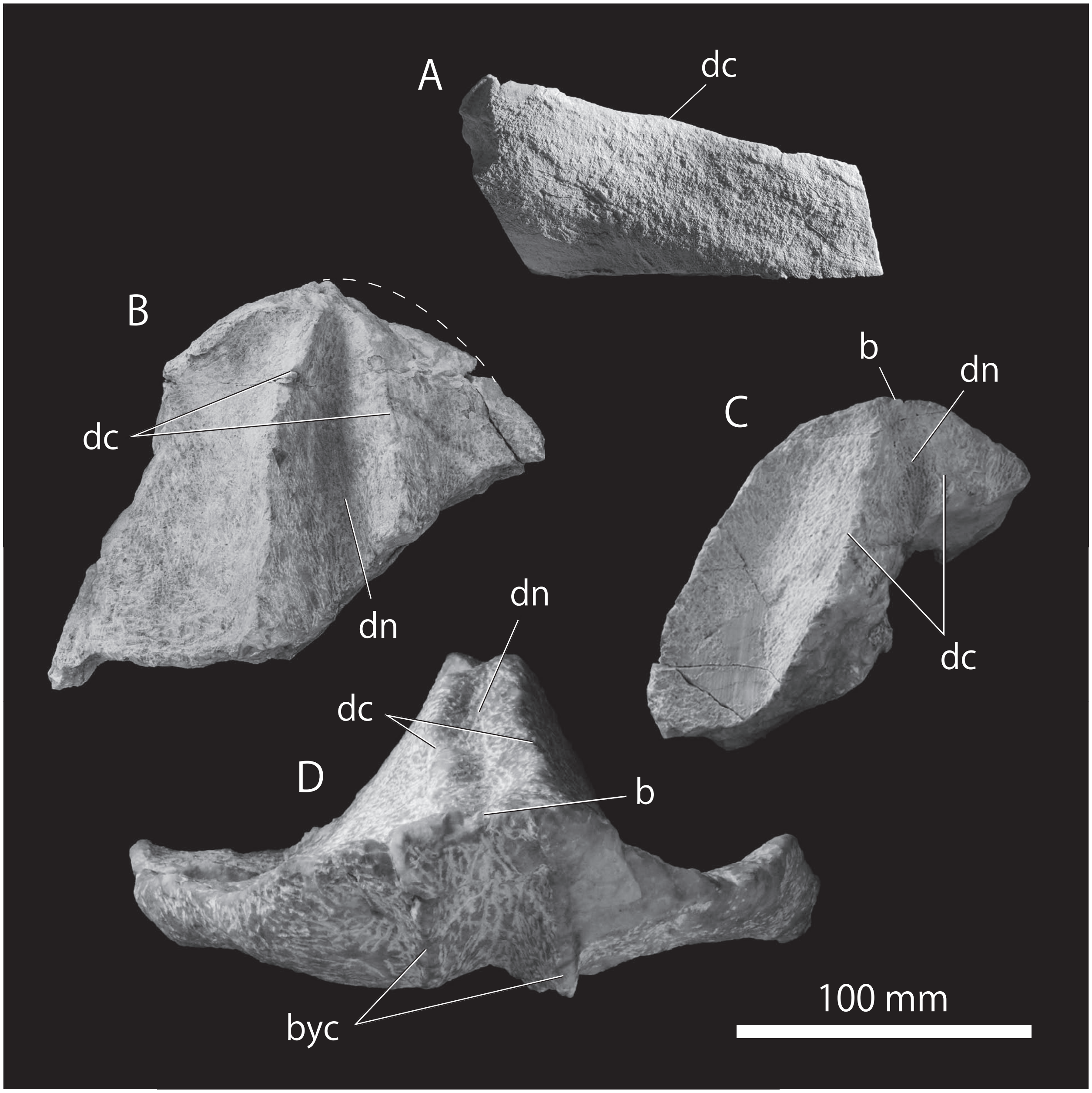

Figure 4. *Shikamaia akasakaensis* Ozaki, 1968 from the middle Permian Akasaka Limestone. **A,** NMNS PM27558, inner lateral view of a fragmentary right valve, showing the dorsal half of the ligament area; **B,** NMNS PM27550, dorsal view of a fragmentary articulated specimen, showing the dorsal niche (dn) and dorsal crest (dc); **C,** NMNS PM27551, dorsal view of the umbonal part of a fragmentary articulated specimen, showing the dorsal niche (dn), beak (b) and dorsal crest (dc); **D,** NMNS PM27553, umbonal view of an articulated specimen, showing dorsal niche and well developed byssal collars (byc).

Neohigashidani and Hatsushikadani valleys in the Neo area of Motosu City, Gifu Prefecture, Japan (Sano, 1988) (Figure 1A). This formation is also an allochthonous limestone body within the Jurassic accretionary complex of the Mino-Tanba Belt (e.g. Isozaki, 1997). The specimen described by Yancey and Ozaki (1986) and an almost complete specimen (NMNS PM27565) in the collection of the National Museum of Nature and Science, Tsukuba were collected at Kurumibashi in the Neohigashidani valley, about 32 km NNE of the type locality of *Shikamaia akasakaensis*. These *Shikamaia*-bearing beds belong to the lower part of the Funabuseyama Formation and to the *Pseudofusulina ambigua* Zone (Sano, 1988). This fusuline zone corresponds to the Kungurian stage of the

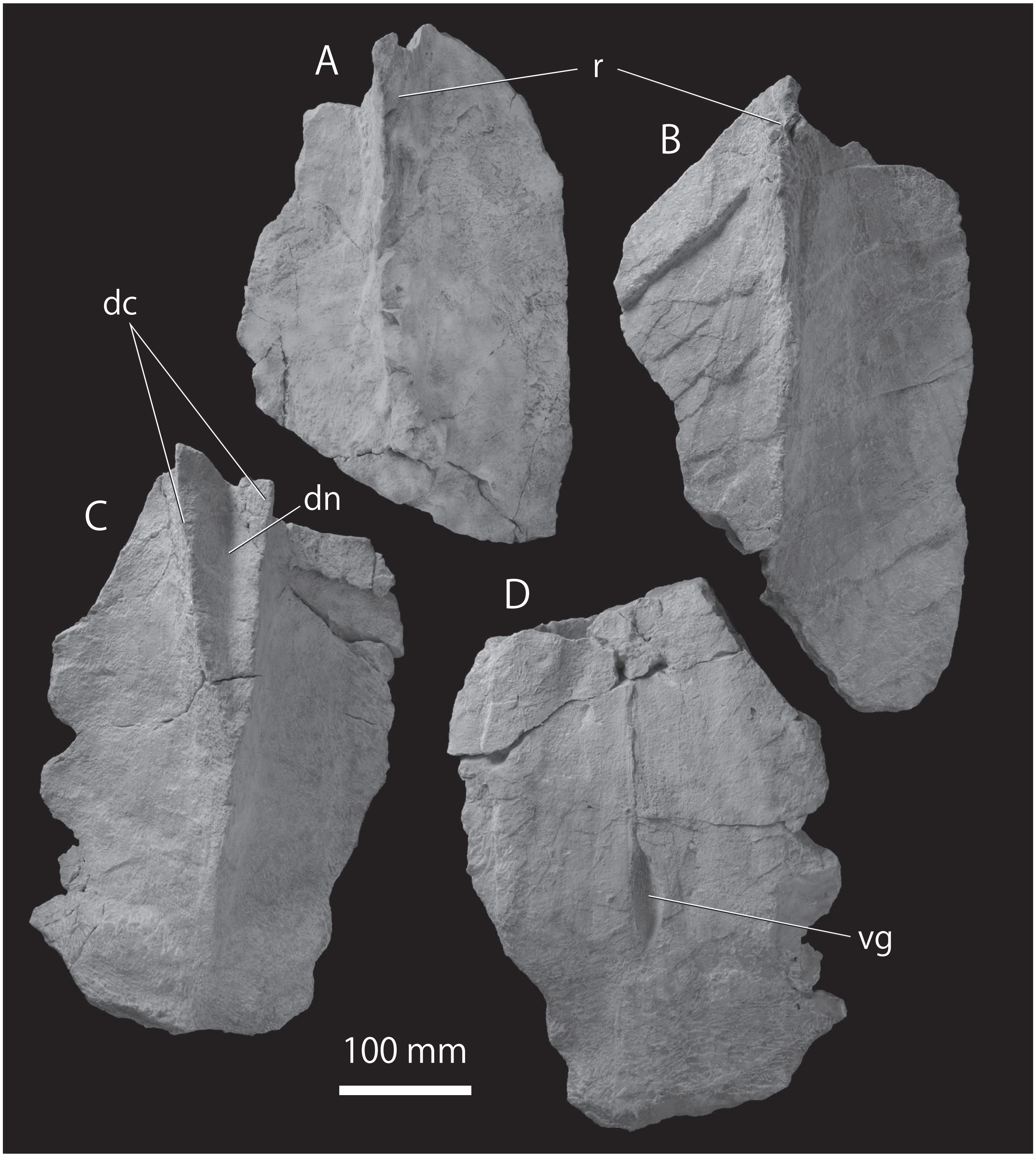

Figure 5. *Shikamaia akasakaensis* Ozaki, 1968 from the middle Permian Akasaka Limestone. **A,** NMNS PM27555, dorsal view of an articulated specimen, preserving the posterior ridge of the dorsal crest (dc) and the intact wing margin of the right valve; **B,** NMNS PM27548, dorsal view of an articulated specimen, preserving the posterior ridge of the dorsal crest, the valves posterior of the ridge and the nearly complete wing margin of the right valve; note that both valves preserve the growth lines; **C, D,** NMNS PM27560, dorsal (C) and ventral (D) views of an articulated specimen, showing the posterior half of the dorsal niche (dn) in C and the elliptical ventral gape (vg) in D.

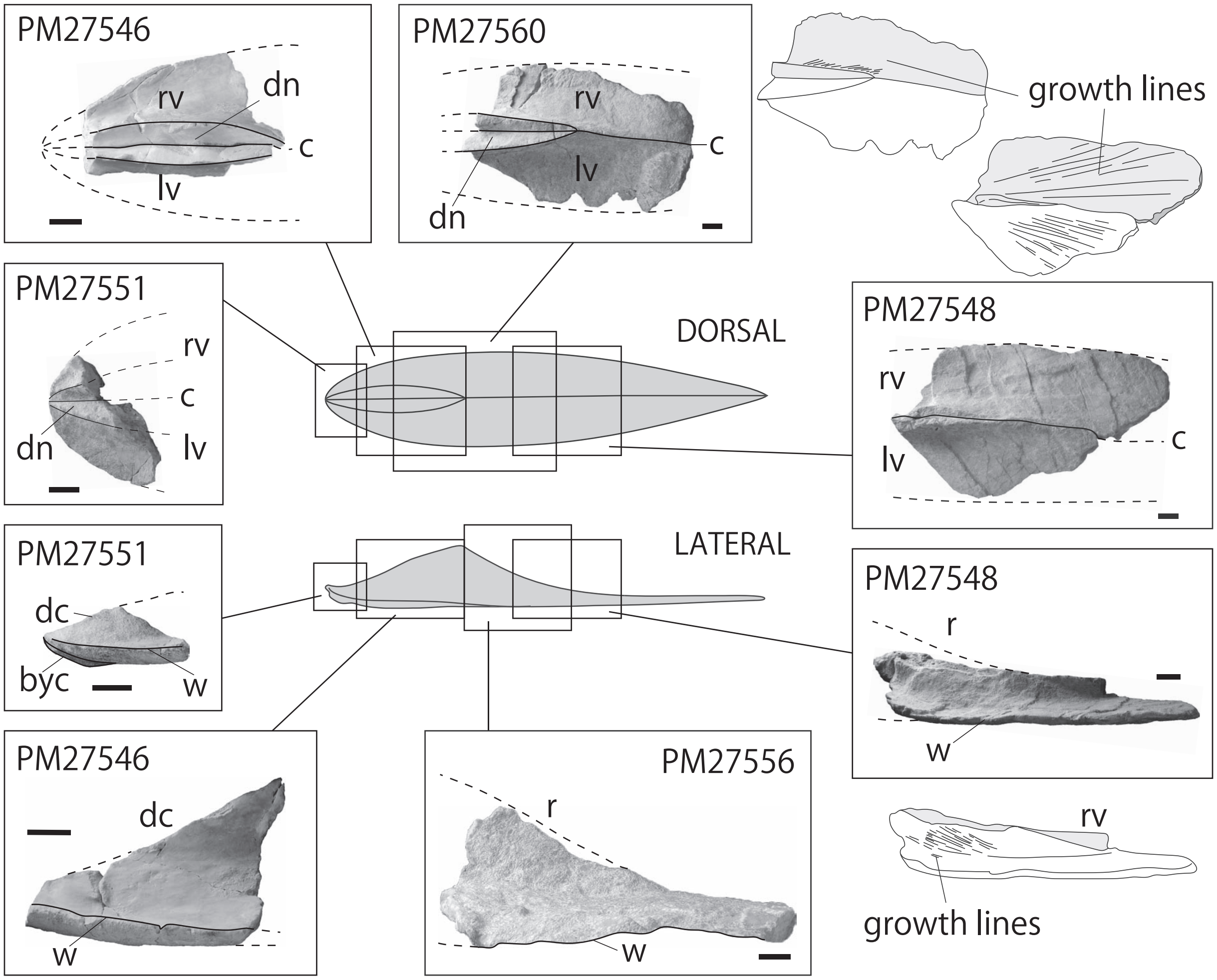

Figure 6. Reconstruction of shell morphology of *Shikamaia akasakaensis* Ozaki, 1968 based on the fragmentary specimens that include key portions of the shell such as beak, wing margin, dorsal niche and dorsal crest. Abbreviations: byc = byssal collar; c = commissure; dc = dorsal crest; dn = dorsal niche; lv = left valve; r = posterior ridge of dorsal crest; rv = right valve; w = wing. Scale bars = 20 mm.

uppermost lower Permian (Sano, 1988; Shen *et al.*, 2013), and the Neo specimens are older than those from the Akasaka Limestone. Sano (1988) and Sano *et al.* (1990) demonstrated that the alatoconchid-bearing beds in the Neo area were deposited in a calm, stagnant, lagoonal mudflat with local patches of coral reefs.

Preparation and shell reconstruction

The shells of the Akasaka specimens are completely recrystallized, and the shell surfaces and fine-grained carbonate matrix are tightly cemented. Additionally, the very large shell size and fragmentary nature of the shells make extraction of whole or even partial shells from the matrix difficult. Natural shell surfaces are preserved in few specimens. To reconstruct the shell form, the first author used air scribers to perform a time-consuming grinding method on the block samples to expose the surface of the shell. Fortunately, the color contrast between the shell and the matrix is sufficient to detect the boundary. More precisely, the color contrast is most distinct between the very thin, dark-colored, prismatic outermost shell layer and the underlying light-colored granular layer. Therefore, the prepared shell surface is not the original shell surface in most prepared specimens, but it is nearly equivalent because the outer prismatic layer is so thin.

The shell reconstruction of *Shikamaia akasakaensis* is based on 19 specimens prepared for this study (Figures 3–5). Because no specimen completely preserves a whole shell, the shell was reconstructed by selecting fragmentary specimens with portions of the shell that could be easily assigned to positions within the alatoconchid bivalve shell (Figure 6). These shell portions include the beak, wing margins, dorsal niche and dorsal crest (par-

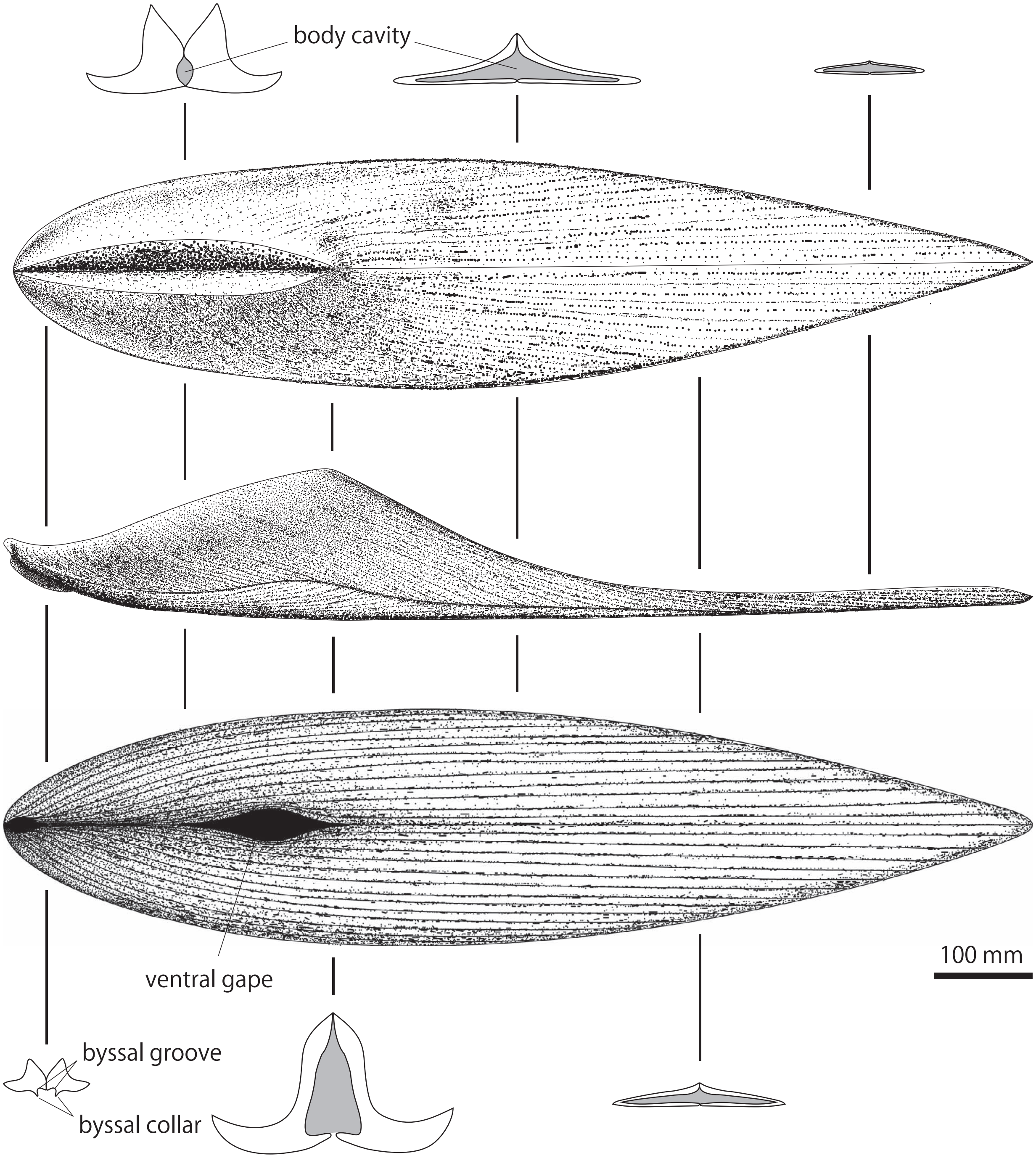

Figure 7. Reconstruction of a fully grown specimen of *Shikamaia akasakaensis* Ozaki, 1968, showing dorsal, left lateral and ventral views of shell, and cross sectional views at the cutting positions indicated by solid lines.

ticularly the highest point of the dorsal crest). The beak is the most easily recognizable portion of the shell of *S. akasakaensis*, and six prepared specimens preserve this portion (Figure 4C). In these specimens, the beaks of the two valves are in contact along the commissure plane irrespective of growth stage. The dorsal niche (a wedge-shaped opening surrounded by the dorsal crests (Yancey and Boyd, 1983)) and the dorsal crests are also key por-

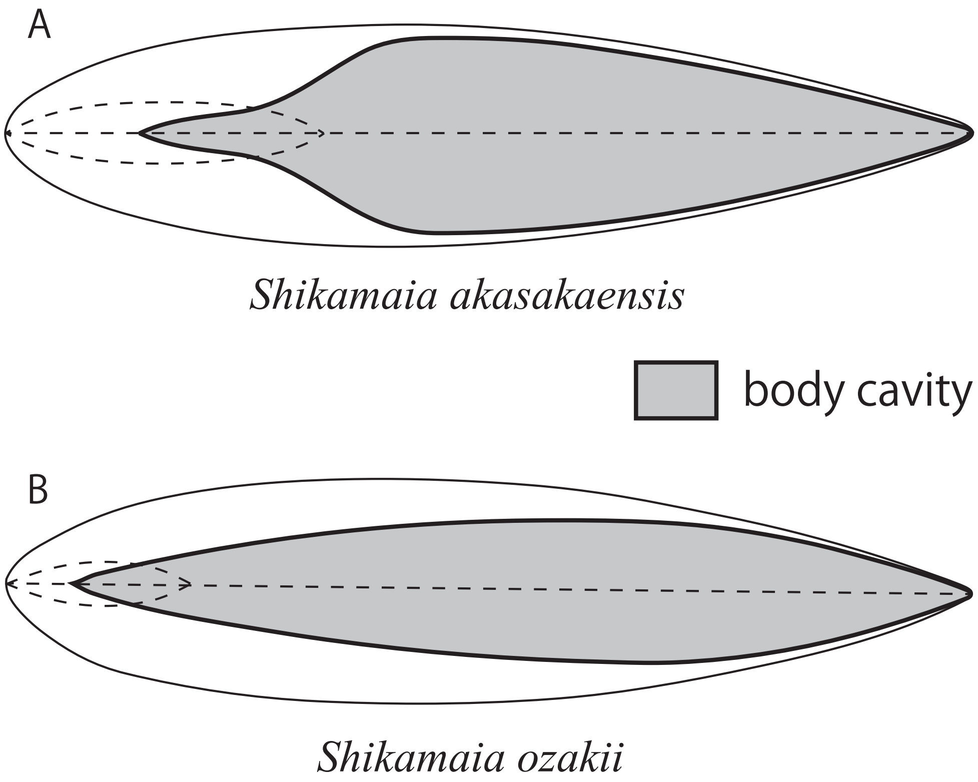

Figure 8. Distribution of the body cavity of *Shikamaia*. **A,** *Shikamaia akasakaensis* Ozaki, 1968; **B,** *Shikamaia ozakii* Asato and Kase sp. nov.

tions to recognize (Figures 4B, C, 5C). In particular, the posterior end of the dorsal crest is the highest portion of the shell. Of the 19 prepared specimens, four preserve this portion (Figure 5C). The intact wing margin is the most important portion to reconstruct the shell outline, particularly if it is combined with other key portions (Figures 3–5). The growth line is a useful character to determine shell orientation despite the fragmentary nature of the specimens (Figure 5B, D).

No specimen preserves the posteriormost end of the shell because this area of the shell appears to be so thin and fragile that it would have been easily destroyed by sediment compaction and/or current movement after death. This part of shell was reconstructed based on a single large, fragmentary specimen that preserves the highest point of the dorsal crest, the posterior slope of the dorsal crest, the intact shell margin of the wing and the growth lines (Figure 5B). In this specimen the wing margin of the right valve is nearly parallel to the commissure, and then gradually curves towards the commissure in the posterior of the shell. Additionally, the growth lines converge toward the commissure line posteriorly. These observations suggest that the posterior shell margin was quite long and pointed at its end. Figure 7 shows the reconstruction of *Shikamaia akasakaensis* obtained with the method described above. Because more key portions were identified from the anterior part of the shell, our reconstruction of *S. akasakaensis* is more reliable in the anterior part of the shell than the posterior. Based on the large size of the shell fragments (Figure 5B), the maximum shell size of *S. akasakaensis* may exceed 1 m in length.

Systematic paleontology

Order Myalinida Paul, 1939
Superfamily Ambonychioidea Miller, 1877
Family Alatoconchidae Termier, Termier and Lapparent, 1973
Subfamily Alatoconchinae Termier, Termier and Lapparent, 1973
Genus ***Shikamaia*** Ozaki, 1968

Synonym.—*Tanchintongia* Runnegar and Gobbett, 1975 (see Yancey and Ozaki, 1986).

Type species.—*Shikamaia akasakaensis* Ozaki, 1968.

Shikamaia akasakaensis Ozaki, 1968

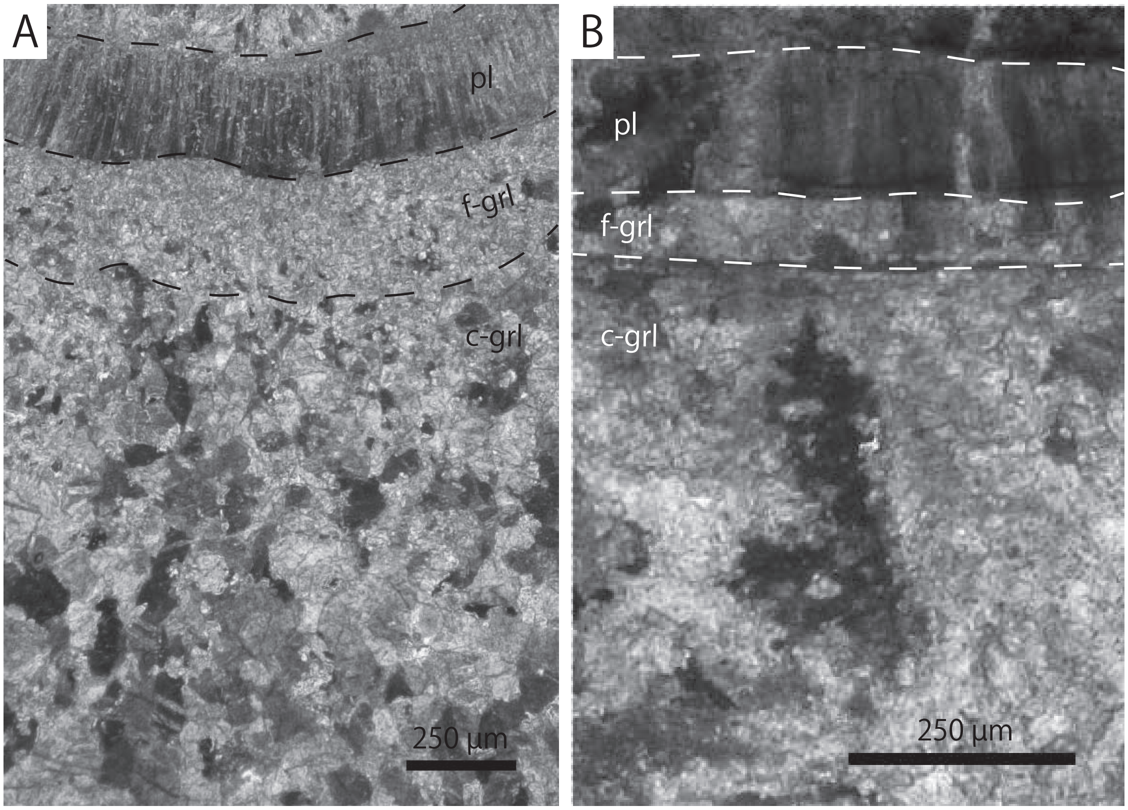

Figure 9. Thin-section photomicrographs of shell of *Shikamaia* under polarized light microscopy. **A,** *Shikamaia akasakaensis* Ozaki, 1968 from the middle Permian Akasaka Limestone; **B,** *Shikamaia ozakii* Asato and Kase sp. nov. from the middle Permian Funabuseyama Formation in the Neo area. Abbreviations: c-grl = coarsely granulated calcite layer; f-grl = finely granulated calcite layer; pl = prismatic layer.

Figures 3–7, 8A, 9A, 10

Shikamaia akasakaensis Ozaki, 1968, p. 28, pls. 7–9; *non* Yancey and Ozaki, 1986, p. 122, figs. 6, 7.

Type.—Lectotype designated by Yancey and Ozaki (1986), NMNS PM16091 (previously registered as YNU 480); two paralectotypes, NMNS PM16092, 16093 (previously registered as YNU 478, 479).

Material examined.—In addition to the three type specimens, 19 specimens, NMNS PM27546–27564, all from the Lower Member of the Akasaka Limestone.

Diagnosis.—A very large *Shikamaia* characterized by appressed terminal beaks, dorsally reflected wing margins in anterior part, large and long dorsal crests as high as shell width and a lanceolate gape in commissure on ventral surface.

Description

Shell outline.—The shell reconstructed in this study is very large, likely over 1 m long in adult, thick (up to 3 cm in the umbonal area), equivalve and strongly compressed dorso-ventrally to form lateral wing-like extensions due to the isoclinal folding of the valves like the modern cardiid *Corculum cardissa*. The articulated valves are elongated antero-posteriorly and likely more than four times longer than wide, tapering more rapidly anteriorly than posteriorly, such that the shell form resembles a bamboo leaf (Figure 7).

The wings in the anterior part of the shell are reflected dorsally at the margin such that the dorsal shell surface is roundly concave (Figure 4D), whereas the ventral shell surface is roundly convex. This concavo-convexity of the shell wing gradually weakens posteriorly, and is almost flat posterior of the posterior end of the dorsal crest.

The dorsal crest is well elevated, and its highest point is located at one-third length posterior from the anterior end, where the shell height is the same as the width of the articulated valves. The dorsal niche is moderately wide and wedge-shaped. The presence of a large cardinal area and the associated large and elevated dorsal crest are diagnostic characters of the genus *Shikamaia* (Figure 3B, C). The dorsal crest is low triangular in lateral view; its highest point is at the middle of the shell in small specimens, whereas it is located more posteriorly in larger speci-

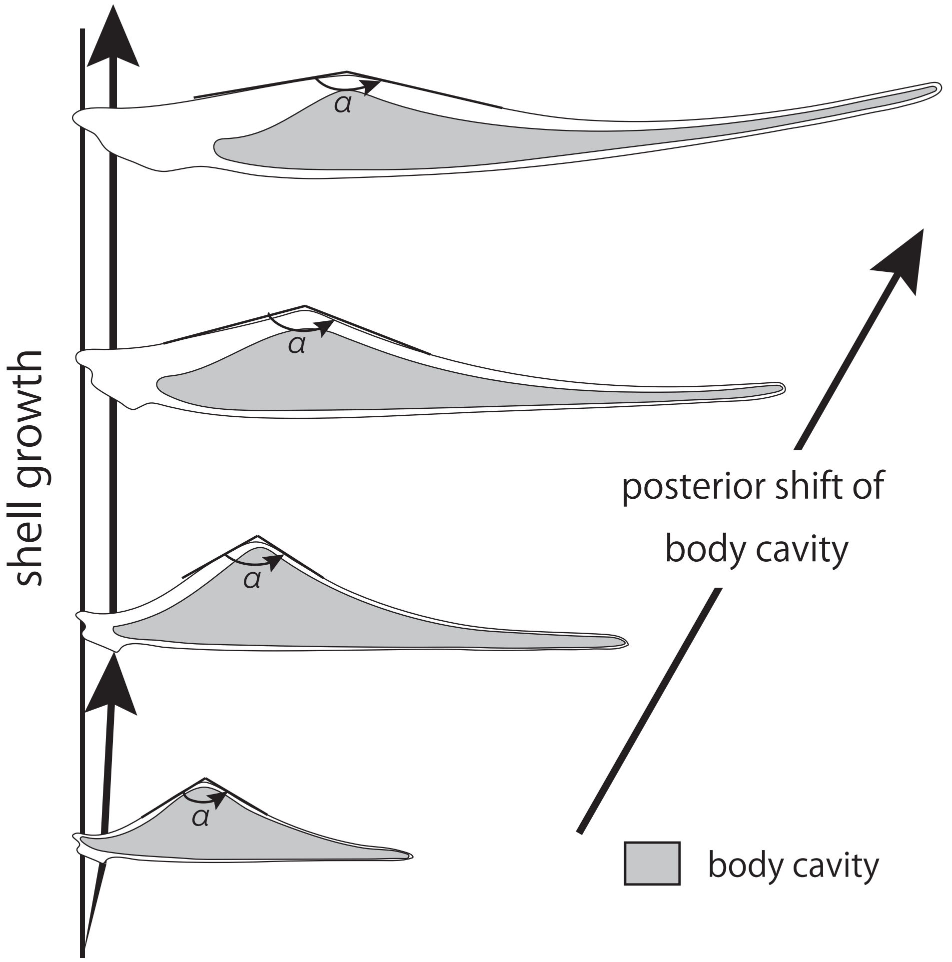

Figure 10. Schematic growth pattern of *Shikamaia akasakaensis* Ozaki, 1968. Note that the drawings at the top and bottom are based on NMNS PM27560 and 27554, respectively, but the two in the middle are not based on real specimens, and also that the angle of the dorsal crest (α) increases during the shell growth in addition to the posterior shift of the body cavity.

mens. Because the shell wall of the umbonal area is the thickest portion in the shell of *Shikamaia akasakaensis*, it is easy to identify even from fragmentary shells. The antero-posterior length of the dorsal crest approximates one-third of the total shell length.

The byssal collar, a unique structure of the Alatoconchidae, is a fold structure of the valves that extends downward from the ventral surface of the beak. It is prominent in small specimens (Figure 4D) but inconspicuous in large specimens (Figure 3A, B). A newly identified structure on the ventral shell surface, unreported in previous studies and only observable in NMNS PM27560, is a gape along the commissure located at a position slightly posterior to the highest point of the dorsal crest on the dorsal surface. This gape is lenticular in shape, 76.5 mm in length and 19 mm in width.

Body cavity.—A remarkable feature of shell growth in *Shikamaia akasakaensis* is the posterior shift of the body cavity during shell growth, which results from the successive infilling of shell material in the umbonal area. Because of this shell growth, the body cavity of *S. akasakaensis* is small relative to the shell size (Figures 7, 8A). In larger specimens, the body cavity starts below the middle point of the dorsal crest, occupying an anteriorly pointed, wedge-shaped narrow space in dorsal view, and then rather abruptly expands laterally into a small space within the isoclinally folded wings (Figure 8A). In smaller specimens, the body cavity extends deep into the beak area (Figure 3C).

Yancey and Boyd (1983) observed the presence of a large posterior adductor muscle scar on the inner shell surface just below the highest point of the dorsal crest in *Shikamaia perakensis* (Runnegar and Gobbett, 1975). The adductor muscle scar of the Akasaka specimen has not yet been identified because of recrystallization and poor preservation. We presume that *S. akasakaensis* has

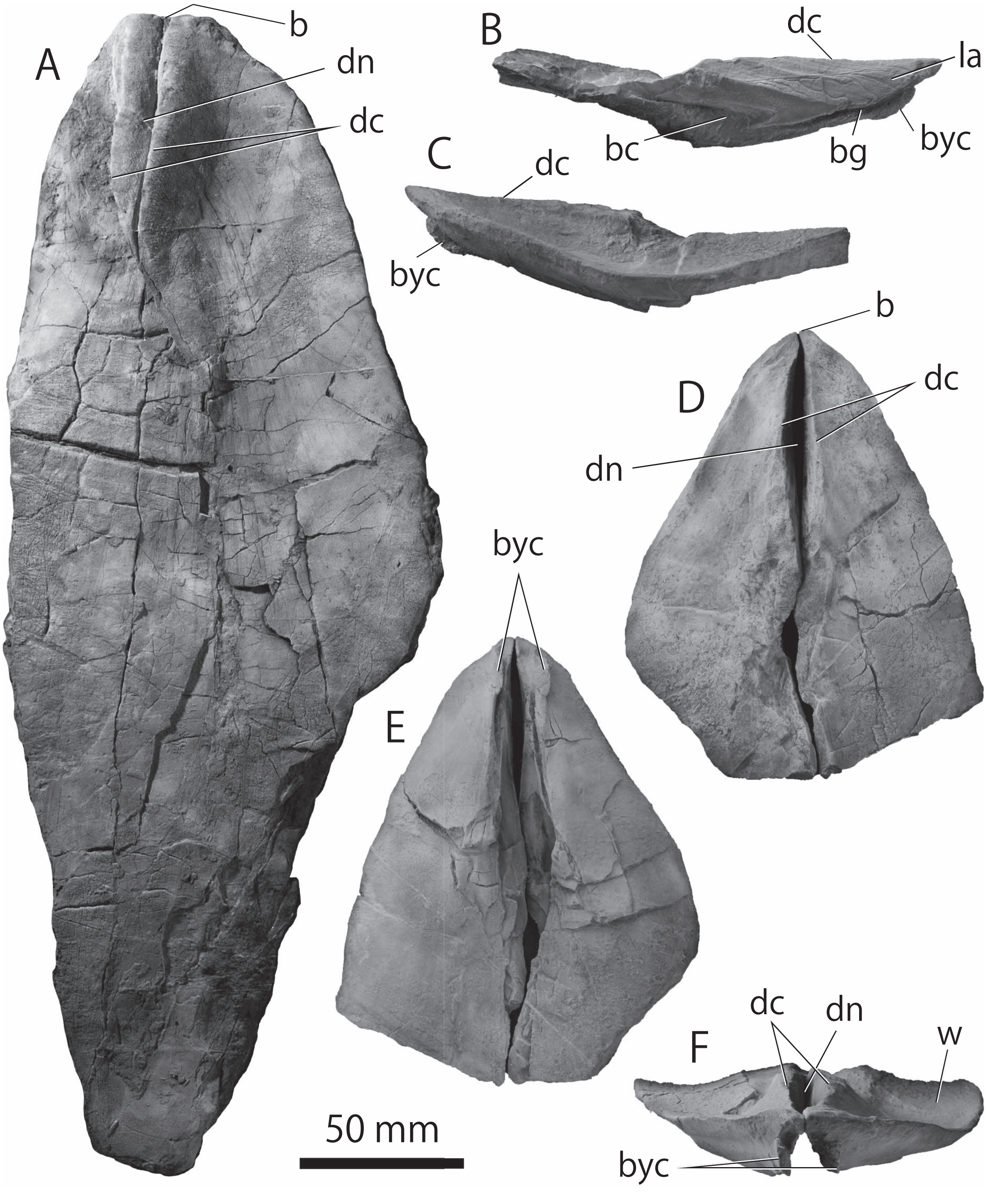

Figure 11. *Shikamaia ozakii* Asato and Kase sp. nov. from the middle Permian Funabuseyama Formation in the Neo area. **A,** NMNS PM27565, dorsal view of the most complete articulated specimen, showing the dorsal niche (dn), commissure, almost intact wing margins and growth lines. Note that the anterior end is missing and the valves are compressed dorso-ventrally. **B–F,** holotype, NMNS PM27769 (formerly YNU 481), anterior part of an articulated shell. B, inner lateral view of the left valve showing the body cavity (bc), dorsal crest (dc), byssal groove (bg), byssal collar (byc) and ligament area (la). C, outer lateral view of the left valve showing byssal collar (byc) near the beak and less elevated dorsal crest (dc). D, dorsal view showing the appressed beaks (b), dorsal niche (dn) and dorsal crest (dc). E, ventral view showing the byssal collar (byc) near the beak. F, anterior view showing the low dorsal niche (dn), dorsal crests (dc), byssal collar (byc) and wings (w).

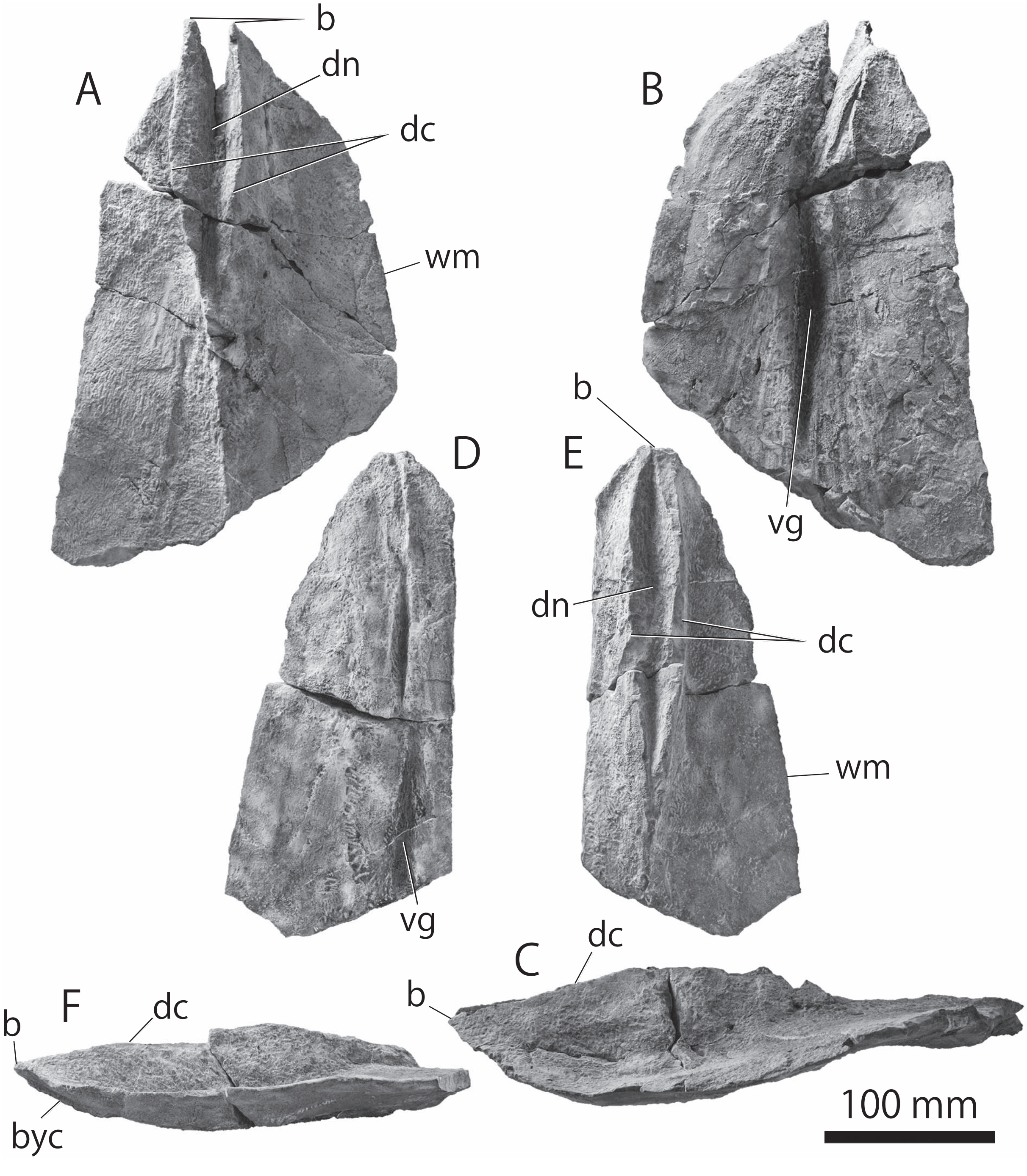

Figure 12. *Shikamaia ozakii* Asato and Kase sp. nov. from the middle Permian Funabuseyama Formation in the Neo area. **A**–**C,** NMNS PM27688, articulated specimen, preserving the anterior half of the shell. A, dorsal view showing the almost complete dorsal niche (dn), dorsal crest (dc) and intact wing margins (wm). Note that the beaks (b) are slightly diverging but that this is due to deformation of the specimen. B, ventral view showing the ventral gape (vg). C, outer lateral view of the left valve showing the less elevated dorsal crest (dc). **D**–**F,** NMNS PM27643, anterior part of an articulated shell. D, ventral view showing the ventral gape (vg). E, dorsal view showing the complete dorsal niche (dc). F, outer lateral view of the left valve showing less elevated dorsal crest (dc) and byssal collar (byc).

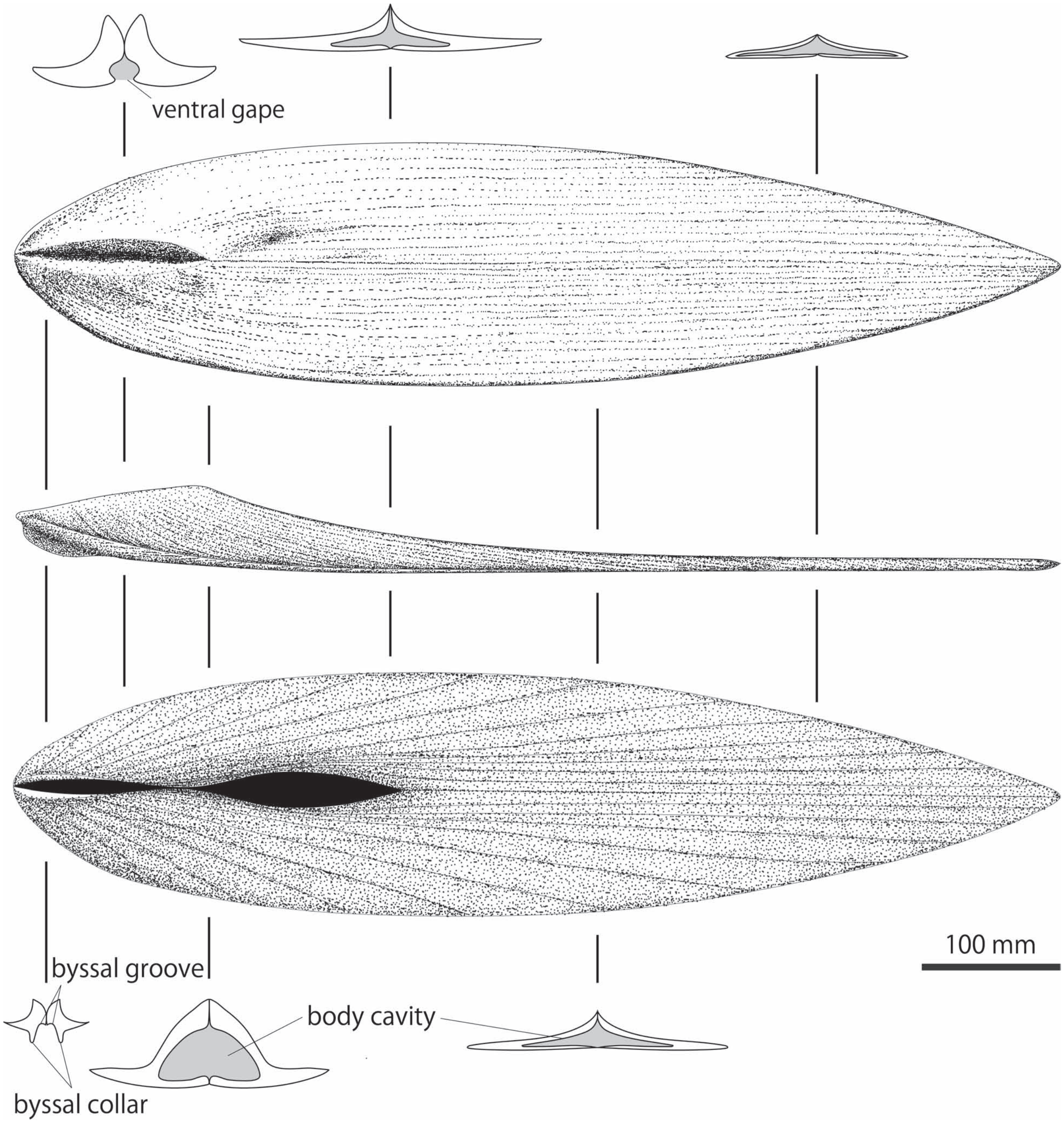

Figure 13. Reconstruction of *Shikamaia ozakii* Asato and Kase sp. nov., showing dorsal, left lateral and ventral views of the shell, and cross-sectional views at the cutting positions indicated by solid lines.

a posterior muscle adductor scar similar to that of *S. perakensis*.

Ligament.—The ligament is one of the most problematic shell morphological structures to observe because of the difficulty of extracting the shell from the limestone matrix. In the Akasaka specimens, the cardinal area has no teeth in the large ligament area between the beak and the hinge line (Figure 3B, C). Some specimens preserve the entire cardinal area, but the detailed surface structures have been lost during preparation (Figure 3B, C). NMNS PM27558 (Figure 4A) is a fragmentary specimen that preserves the intact surface of the cardinal area, where obscure, anteriorly inclined fine lines are present. Yancey and Ozaki (1986) showed that in the Neo specimens,

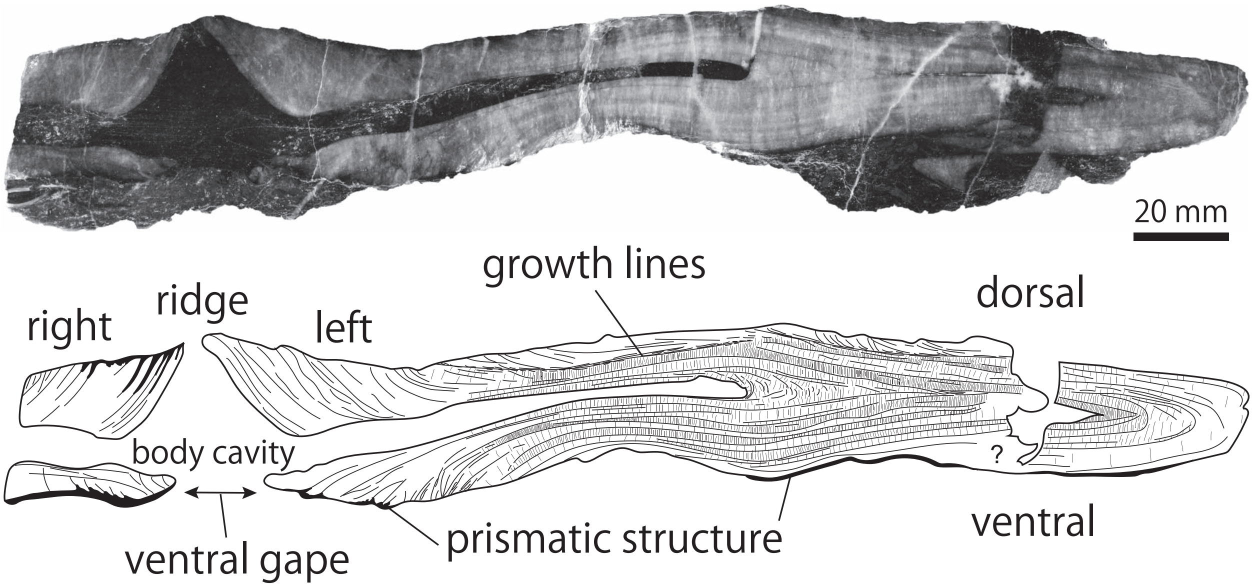

Figure 14. Polished transverse cross-section (above) of a shell of *Shikamaia ozakii* Asato and Kase sp. nov. (NMNS PM27780) from the middle Permian Funabuseyama Formation in the Neo area and its schematic sketch (below), showing the distribution of the outer prismatic layer and the two subadjacent granulated calcite layers (not separated), and shell growth pattern. This section was cut approximately at the middle portion of the shell.

Shikamaia has a modified ligament groove in only the lower half of this area. The obscure lines seen in NMNS PM27558 appear to be the growth lines above the ligament; therefore the ligament is not preserved in this specimen. Indeed, the lower part of the ligament area was lost when the specimen was collected. We assume that like in the Neo specimens, the cardinal area has a ligament area below the finely striated part in the Akasaka specimens.

Shell microstructure.—Ozaki (1968) observed a thin layer composed of a “laminar structure” that extends obliquely with acute angles against the outer surface. Later authors recognized two layers in *Shikamaia akasakaensis* and certain other alatoconchids: a thin outer prismatic layer and a thick layer with a large granular structure (Yancey and Boyd, 1983; Yancey, 1985; Isozaki, 2006; Isozaki and Aljinović, 2009). In this study, thin-section observations under a polarized light microscope have revealed that the shell of *S. akasakaensis* consists of three layers (Figure 9A). The outermost layer is nearly translucent in the thin section under open nicols, and is composed of an aggregation of straight or weakly curved prismatic crystals, 500 µm in length and 20–30 µm in diameter, arranged nearly perpendicular to the shell surface (pl in Figure 9A). The second layer, 500 µm in thickness, is composed of a fine-grained granular structure with grains approximately 20 µm in diameter (f-grl in Figure 9A). The third layer, composed of a coarse-grained granular structure of calcite, is very thick, about 20 mm near the beak, 10 mm in the middle and 5 mm in the posterior portion of the shell (c-grl in Figure 9A). The calcite grains of this structure are approximately 50 µm in diameter. These second and third layers spread widely within the shell far beyond the expected position of the adductor muscle scar, which suggests that the two layers are part of the outer layer above the myostracum in *S. akasakaensis*. We have not identified the myostracal and inner layers; it is likely that these two layers are very thin.

Shell growth.—Although available specimens are limited in number, a rough sketch of ontogenetic change in the shell form of *Shikamaia akasakaensis* can be deduced. The most remarkable change is the backward shifting of the body cavity, as well as the concomitant changes in shell form. In small specimens (e.g. NMNS PM27559, Figure 3C), the shell is thin, the ligament area narrow, and the body cavity is deeply excavated and extends anteriorly almost to the beak. During shell growth, the shell of the umbonal area becomes thicker, the ligament area becomes wider, and the anterior part of the body cavity shifts posteriorly, such that the umbonal area gradually becomes more robust (e.g. the large specimen NMNS PM27546, Figure 3A, B). The thickening of the umbonal and ligament area is caused by successive addition to the innermost coarse-grained shell layer in the ligament area and the adjacent area of the shell. As the result, the body cavity in the wing is completely filled with shell material in the anterior portion of the shell (Figure 10).

Changes in shell form associated with this growth are the backward shifting of the highest point of the dorsal

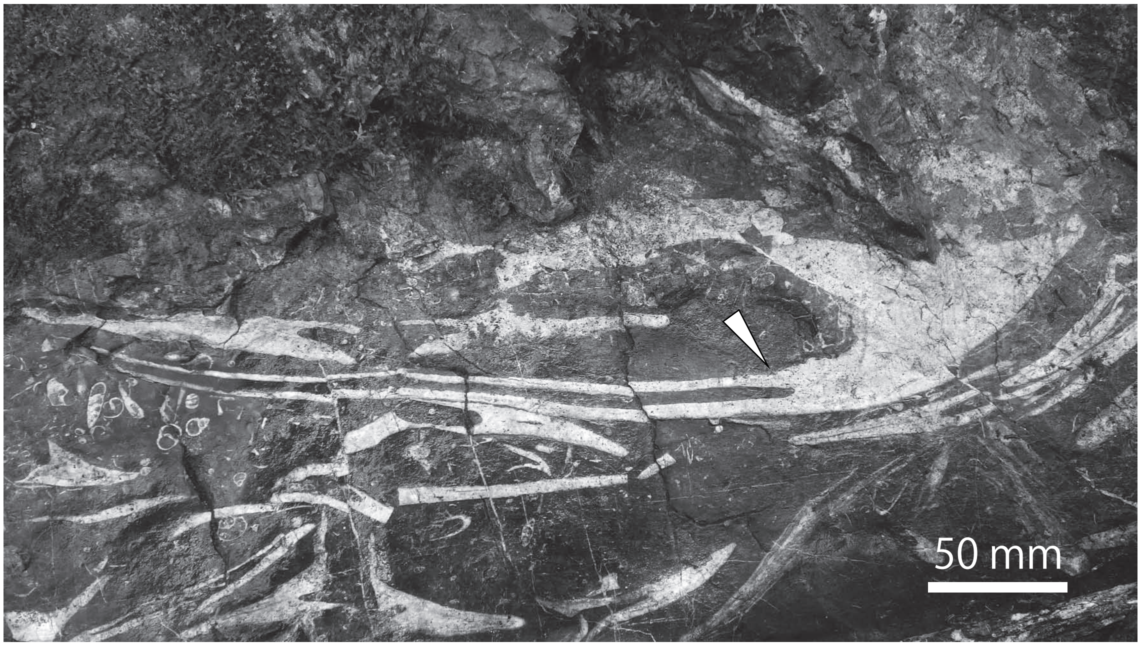

Figure 15. Cross sectional views of *Shikamaia ozakii* Asato and Kase sp. nov. on an outcrop of the middle Permian Funabuseyama Formation in the Neo area. One individual (indicated by arrow) cut slightly obliquely from the commissure line is about 30 cm long, showing the light-colored grained calcite layers spread over the posterior end of the shell.

crest relative to the shell length and the increase of the ridge angle on the dorsal crest (Figure 10). The ridge angle is defined as the angle between the anterior and posterior slopes of the dorsal crest. As shown in Figure 10, this angle becomes larger in accordance during the shell growth with the increase in the distance from the anterior end to the highest point of the dorsal crest.

The umbonal angle of both valves, here defined as the angle between the shell wings (perpendicular to the umbonal angle in bivalves), becomes larger during the shell growth. This ontogenetic change is well observed among specimens of different growth stages. For example, NMNS PM27559 (Figure 3C, D) is a young and slender specimen, and its umbonal angle is about 70°. NMNS PM27551 (Figure 4C) is a fragmentary articulated specimen with the umbonal area preserved. This specimen appears to be much larger than NMNS PM27559 because the ligament area is quite wide. An additional example is NMNS PM27550 (Figure 4B), which also appears to be a large specimen based on the width of the ligament area. The umbonal angle is 150° in this specimen.

Shikamaia ozakii Asato and Kase sp. nov.

Figures 8B, 9B, 11–15

Shikamaia akasakaensis Ozaki, 1968. Yancey and Ozaki, 1986, p. 122, figs. 6, 7.

Type.—Holotype, NMNS PM27769 (formerly YNU 481), illustrated by Yancey and Ozaki (1986, figs. 6, 7), from the Funabuseyama Formation at the Kurumibashi Bridge in the Neo area. Paratype, NMNS PM27565 from the same locality.

Etymology.—Named after the late K. Ozaki of Yokohama National University, the author who first described *Shikamaia akasakaensis*.

Diagnosis.—A large *Shikamaia* similar to *Shikamaia akasakaensis* in overall shell outline differing from the latter in having less concavo-convex wings in the anterior part and short and low dorsal crests.

Additional shell description

Yancey and Ozaki (1986) described the anterior part of the shell and the cardinal and ligament structures in detail. NMNS PM27565 (Figure 11A) is one of the most complete specimens found of this species. We describe the overall shell morphology based on NMNS PM27565 and the holotype. For detailed description of the cardinal and ligament structures and the byssal collar, see Yancey and Ozaki (1986).

Shell outline.—The shell reconstructed in this study is elongated antero-posteriorly and strongly compressed dorso-ventrally, and is more than four times longer than wide. Its shape resembles that of a bamboo leaf (Figure 13).

The wing margin is weakly upturned ventrally, and the ventral and dorsal shell surfaces are weakly concave and convex, respectively, in the anterior portion of the shell. These dorsal and ventral convexities gradually weaken posteriorly, such that the shell wings posterior of the dorsal crest are nearly flat. The dorsal crest is much lower than those of *Shikamaia akasakaensis*, and the highest point is located at one-fifth to one-sixth length posterior from the anterior end, where the shell height is nearly half the articulated shell width. The dorsal crest is approximately one-sixth the length of the total shell. The ventral gape is a lenticular opening along the commissure, 114 mm in long and 24 mm in wide, and is located slightly posterior to the highest point of the dorsal crest on the dorsal surface (Figures 12B, D, 13).

Body cavity.—The extension of the body cavity within the shell of *Shikamaia ozakii* Asato and Kase sp. nov. was ascertained by observing cross-sections of a number of specimens exposed in the limestone in outcrop. The reconstruction of the body cavity shown in Figure 8B therefore may not be completely accurate. Like in *S. akasakaensis*, the body cavity is small relative to the shell size and starts to open below the midpoint of the dorsal crest. However, the body cavity of this species expands more gradually laterally toward the shell posterior because of the widespread occurrence of shell material infilling in the shell wings.

Shell microstructure.—Like that of *Shikamaia akasakaensis*, the shell of *S. ozakii* Asato and Kase sp. nov. is comprised of three layers: a thin outermost prismatic layer, a thin, fine-grained granular layer and a thick, coarse-grained mosaic layer (Figure 9B). However, unlike that of *S. akasakaensis*, the shell of *S. ozakii* Asato and Kase sp. nov. preserves shell growth lines (Figure 14), which suggests that the shell of *S. ozakii* Asato and Kase sp. nov. is more intact than that of *S. akasakaensis*. The growth lines clearly show the successive infilling of the two granular layers within the shell. Interestingly, the shell of these granular layers, in contrast to the black color of the outermost prismatic layer, is snowy white, particularly on fractured surfaces (Figure 15). Although the original shell microstructure of these granular layers remains unknown, we suggest that the shell of the granular layers may have been poor in organic content, similar to the chalky deposits in modern oyster shells. If this was the case, the shell of *S. ozakii* Asato and Kase sp. nov. would be lightweight.

Discussion

Comparison

Our reconstruction of the overall shell morphology and shell growth pattern of *Shikamaia akasakaensis* from the Akasaka area enables species-level comparison not only between the specimens from the Akasaka and Neo areas but also between *S. akasakaensis* and other alatoconchid species. This study shows that the specimens from the Akasaka and Neo areas exhibit nearly identical shell profiles and therefore are difficult to differentiate based on this shell character alone. In regard to shell size, Yancey and Ozaki (1986) estimated a maximum shell length of 90 cm or more for "*S. akasakaensis"* (= *Shikamaia ozakii* Asato and Kase sp. nov. in this study) from the Neo area, and further suggested that the shell length for this species could reach 1 m or more. Yancey and Ozaki (1986) estimated a maximum shell length of over 1 m for *S. akasakaensis* from the Akasaka Limestone, which is concordant with our result. In contrast, they considered the shell length/width ratio to be 3.5:1 and found the largest specimen with a shell maximum width of 20 cm, from which they estimated a shell length of around 70 cm for this specimen. Our reconstruction of the shell for the Neo specimens is based mainly on NMNS PM27565, the most complete specimen yet found. Based on the reconstruction of this specimen, we obtained a length/width ratio of 4:1; therefore, our estimate of the shell length is about 80 cm for the specimen they observed. Whichever shell length/width estimation is more accurate, it is evident that the alatoconchid specimens from the Akasaka area are slightly larger than those from the Neo area.

The most significant differences in shell characters that warrant separation of *Shikamaia ozakii* Asato and Kase sp. nov. from *S. akasakaensis* are the length and height of the dorsal crest and the concavo-convexity of the wings in the anterior portions of the shells. In *S. akasakaensis*, the dorsal crest is elevated much higher than in *S. ozakii* Asato and Kase sp. nov. Because of this greater elevation in *S. akasakaensis*, the dorso-ventral shell thickness is nearly equal to the shell width at the highest point of the dorsal crest, whereas it is less than half of the shell width in *S. ozakii* Asato and Kase sp. nov. In addition to these differences, the dorsal crest occupies about 20% of the shell length in *S. ozakii* Asato and Kase sp. nov. compared to 30% in *S. akasakaensis*, and the concavo-convexity of the shell wings in the anterior portion is weaker in *S. ozakii* Asato and Kase sp. nov. than in *S. akasakaensis*, which gives a more flattened shell profile in *S. ozakii* Asato and Kase sp. nov. relative to that in *S. akasakaensis*.

Shikamaia perakensis, which was once the best studied alatoconchid species and was the type species of the nominal monotypic genus/subgenus *Tanchintongia* (Runnegar and Gobbett, 1975; Yancey and Boyd, 1983), exhibits a bamboo leaf-shaped shell form similar to those of *S. akasakaensis* and *S. ozakii* Asato and Kase sp. nov., except that the beaks diverge from the commissure line as illustrated by Runnegar and Gobbett (1975) and Yancey and Boyd (1983). In particular, the dorsal crests of *S. perakensis* are highly elevated as in *S. akasakaensis*. However, Yancey and Ozaki (1986) stated that the presence of diverging beaks in *S. perakensis* was only an assumption. A juvenile shell of *S. perakensis* has appressed beaks (Yancey and Boyd, 1983, pl. 62, figs. 5–9). If the divergent beaks were truly present in *S. perakensis*, these beaks would therefore have appeared in later growth stages. No other described alatoconchid has such diverging beaks, but a large yet undescribed alatoconchid from the Middle and Upper members of the Akasaka Limestone appears to have diverging beaks (unpublished observation). Additional sampling and study are needed to clarify the relationship between *S. perakensis* and *S. akasakaensis*.

Paleoecology

Previous studies have suggested that alatoconchid bivalves were epifaunal recliners on soft sediment surfaces in shallow marine environments because their wing-like shells may have acted like snowshoes to prevent the shells from sinking into the soft sediment and/or as an anchor to prevent overturning (Runnegar and Gobbett, 1975; Yancey, 1982, 1985; Yancey and Boyd, 1983; Seilacher, 1984; Yancey and Ozaki, 1986; Isozaki, 2006; Isozaki and Aljinović, 2009; Vermeij, 2013). We concur with this interpretation.

Another remarkable trait interpretation for alatoconchid bivalves is a possible association with photosymbiotic microbes within the soft tissues of the animal, similar to modern cardiids and tridacnids (Yancey and Boyd, 1983; Seilacher, 1990; Aberhan and von Hillebrandt, 1999; Yancey and Stanley, 1999; Isozaki, 2006; Isozaki and Aljinović, 2009; Yancey *et al*., 2009). This supposition is based on three facts: (1) alatoconchid shells are extraordinary large and thick among Paleozoic bivalves, (2) the shell form of *Shikamaia* is similar to that of the modern photosymbiotic cardiid bivalve *Corculum cardissa*, and (3) the thin outermost prismatic shell layer of *Shikamaia* could have been translucent enough to be penetrated by ambient sunlight. In *C. cardissa*, the upward-facing dorsal valve surfaces have many radially arranged triangular “windows” that are composed of light-conducting fibrous prisms extending from beneath the thin exterior prismatic layer to the interior shell surfaces (Kawaguchi, 1950, 1983; Seilacher, 1973; Vogel, 1975; Watson and Signor, 1986; Ohno *et al*., 1995). Watson and Signor (1986) observed more light transmission in the “windows” than in the part of the shell without such “windows”. However, flattened and semitranslucent valves are not necessarily reliable evidence for photosymbiosis in bivalves because extant bivalves with translucent shells that live in soft sediments, such as placunids, galeommatoideans, and tellinids, do not harbor photosymbionts in their soft tissues (Savazzi, 2001). Our study shows the presence of thick layers of granular crystals subjacent to the very thin outermost prismatic layer in *Shikamaia akasakaensis* and *S. ozakii* Asato and Kase sp. nov.; these layers are located above the myostracum layer and are likely to extend widely to the posterior part of the shell. Even in the posterior marginal area, the shell is quite thickly lined with these granular layers. Additionally, we have not recognized any window-like structures of prismatic crystals, as seen in *C. cardissa*, in the valves of *S. akasakaensis* or *S. ozakii* Asato and Kase sp. nov. These findings strongly suggest that ambient sunlight could not penetrate through the valves of these *Shikamaia* species sufficiently for microbial symbionts to conduct photosymbiosis. Therefore, it is highly unlikely that the “*Corculum* model” is applicable for *Shikamaia*.

In contrast with *Corculum cardissa*, several modern clams belonging to the Cardiidae and Tridacnidae employ photosymbiotic modes of life without semitranslucent shells. For example, the giant, very thick-shelled tridacnids harbor zoothanthellae in their hypertrophied mantle lobes (Yonge, 1936). Tridacnids gape their shell about 20°, and extend their mantle lobes over the outer margin along the long, upward-facing and strongly folded ventral valve margin such that the exposed mantle edges can receive sufficient sunlight (Yonge, 1936). In *Shikamaia akasakaensis* and *S. ozakii* Asato and Kase sp. nov., the functional ligament is short, extends postero-dorsally, and occupies the ventral half of the cardinal area, positioned such that, as pointed out by Yancey and Ozaki (1986), the valves could likely gape on the ventral side more than on the dorsal side when the muscle was relaxed. For *S. ozakii* Asato and Kase sp. nov., we estimated the valves to gape around 5° along the hinge axis based on observations of the articulated holotype. It is therefore unlikely that the valves of *S. akasakaensis* and *S. ozakii* Asato and Kase sp. nov. could gape as widely as those of tridacnids.

In addition to *Corculum*, the reef-associated cardiid fragine genera *Fragum* and *Lunulicardia* host zooxanthellae photosymbionts in their mantle edges and gills (Kawaguti, 1950, 1983; Ohno *et al*., 1995; Kirkendale, 2009, etc.). The modes of life of three *Fragum* species, *F. unedo* (Linnaeus, 1758), *F. fragum* (Linnaeus, 1758) and *F. loochooanum* Kira, 1959, have been studied extensively by Kawaguti (1983) and Ohno *et al*. (1995). When these bivalves burrow, the valves of these three species become completely immersed in bioclastic sand with their flattened posterior valve surfaces kept just beneath a thin cover of sediment. In *F. unedo*, the zooxanthellae-bearing mantle edges spread over the sediment from the slightly open valve commissure to form a fan-shaped lobe (Kawaguti, 1983; Ohno *et al*., 1995), whereas in *F. fragum* and *F. loochooanum* the tentacled mantle edges extend very slightly from the valve commissure (Ohno *et al*., 1995). *Shikamaia* may have postured in the same manner as do these photosymbiotic fragine species because even a very slight opening of the valves may have been sufficient to spread the mantle edges out from the shell commissure. However, unlike the tridacnids, these *Fragum* species do not show conventional shell traits adapted to a photosymbiotic mode of life because non-photosymbiotic fragine species have nearly identical shell forms. Vermeij (2013) observed that the robust and smooth posterior valve margins of the photosymbiotic *Fragum* species by the deposition of inductural deposits is an indication of the expansion of the mantle over the posterior portion of the shell surfaces. This structure is well known in the purported photosymbiotic fragine species *Protocardia* (*Pachycardia*) *stantoni* (Wade, 1925) from the upper Cretaceous of Tennessee (Schneider and Carter, 2001). However, we do not observe such reflected shell margins in *Shikamaia akasakaensis* and *S. ozakii* Asato and Kase sp. nov. (Figure 14). However, this feature is not always present in other photosymbiotic fragine bivalves. We consider the "fragine model" to be more reasonable for a photosymbiotic interpretation of *Shikamaia*, but this interpretation remains an assumption.

We do not consider photosymbiosis to be the only plausible mode of life of *Shikamaia*; we suggest two additional possible interpretations: one is chemosymbiosis, and the other is suspension feeding. Both *Shikamaia akasakaensis* and *S. ozakii* Asato and Kase sp. nov. have an elliptical gape along the commissure on the ventral shell surface. We identified the same structure in a yet undescribed large alatoconchid species from the Middle and Upper members of the Akasaka Limestone, which suggests that this structure is a common shell character among alatoconchid bivalves. This gape is also found in bivalves of certain groups along the commissure of the ventral margin (e.g. *Barbatia* and *Brachidontes*), along the antero-dorsal margin (*Tridacna*), or in the umbonal area of the right valve (anomiids) (e.g. Stanley, 1970). These gapes function as openings from which bundles of byssal threads extend to attach firmly to a hard substratum. Although *Shikamaia* has a byssal opening below the beak, it is possible to interpret that the byssal groove opening and ventral gape were produced by the same tissue at different stages of the life cycle. In other word, the byssal groove is developed during juvenile growth while the ventral gape is an adult feature in the same part of the body cavity. Another interpretation is that the gape is an opening from which the soft-bodied animal extends its foot to burrow, but this behavior is also unlikely because bivalves do not require such a gape during burrowing, but can instead burrow with their valves open. Additionally, burrowing into the sediment by foot is irreconcilable with the snowshoe strategy of *Shikamaia*.

We instead interpret that the gape may have functioned as an opening for the mantle cavity to perform chemosymbiosis. Similar to the modern lucinid bivalves, *Shikamaia* may have pumped up H_2S-rich seawater up from deeper sediment layers by ciliary movement to nourish chemoautotrophic bacteria within the animal's soft tissue, similar to the modern chemosymbiotic lucinid bivalves. The preferential occurrence of *Shikamaia* and other alatoconchids in bituminous, often oily and odorous black wackestone to lime mudstone facies (Yancey and Boyd, 1983; Sano, 1988; Kiessling and Flügel, 2000; Isozaki, 2006; Aljinović *et al*., 2008; Isozaki and Aljinović, 2009; Udchachon *et al*., 2014) supports this chemosymbiosis scenario. However, these taxa also occur in light-gray to gray wackestone/packstone facies in Japan, Malaysia and Tunisia (Runnegar and Gobbet, 1975; Newell *et al*., 1976; Boyd and Newell, 1979; Kobayashi, 2011; Udchachon *et al*., 2014). To verify this working hypothesis, detailed sedimentological analysis of alatoconchid-bearing limestone is needed.

The scenario that alatoconchids are non-photosymbiotic, non-chemosymbiotic, normal suspension-feeding bivalves cannot be completely eliminated. In the Akasaka Limestone, alatoconchids occur in association with extraordinarily large mollusks, crinoids and brachiopods (Hayasaka and Hayasaka, 1953; Nützel and Nakazawa, 2012). In the Lower Member, *Shikamaia akasakaensis* is associated with a yet undescribed large species of the pleurotomarioidean *Euconospira* (in the private collection of M. Hori), a yet unstudied large crinoid(s) with a stem diameter of up to 8 cm (in the collection of Akasaka Fossil Museum), together with normal-sized mollusks. Extraordinarily large mollusks and an alatoconchid also occur in the Middle and Upper members of the Akasaka Limestone together with diverse normal-sized and microscopic mollusks; for example, the bellerophontid gastropod (or monoplacophoran) *Bellerophon jonesianus* DeKoninck, 1863 reaches 18 cm in diameter, the neritopsidean gastropod *Naticopsis wakimizui* Hayasaka, 1943 reaches 19 cm in width, the pleurotomarioidean gastropod *Nipponomaria yokoyamai* (Hayasaka, 1943) reaches 25 cm in width, the goniasmatid *Akasakiella yabei* (Hayasaka, 1943) reaches 40 cm in length, two scaphopods are both *ca.* 20 cm in length, the grammyisiid bivalve *Alura elegantissima* (Hayasaka, 1925) reaches 24 cm in width, an undetermined grammyisiid bivalve reaches 35 cm in width, and the lirocetarid nautiloid *Coelogasteroceras giganteum* Nakazawa, 1960 reaches 25 cm in diameter (Hayasaka, 1925, 1943; Nakazawa, 1960; Tokai Fossil Research Club, 1974; Nützel and Nakazawa, 2012; Asato *et al*., 2016; unpublished data). These large-sized species may have had a variety of feeding methods, such as grazing, suspension feeding and carnivory, based on those of their modern relatives. Vermeij (2011, 2012) extensively investigated the history of gigantism in Cenozoic marine benthic mollusks, and showed that the maximum body size of benthic mollusks is a good proxy for benthic primary productivity available for these species. Although the benthic food source is not yet known, the occurrence of very large invertebrate species in the Akasaka Limestone suggests the presence of large amount of food on this shallow marine carbonate platform atop a mid-oceanic seamount. Global high productivity in ocean surface water during the Guadalupian low sea-level/cooling Kamura event has been strongly suggested by carbon isotope studies (Isozaki *et al*., 2007a, b). Therefore, the possibility cannot be disregarded that these alatoconchids grew to such large sizes utilizing such food resources without adopting photo- and chemosymbiosis.

Conclusions

1. The overall shell form of the unusually large and aberrantly shaped alatoconchid bivalve *Shikamaia akasakaensis* Ozaki, 1968, a taxon previously known only from fragmentary specimens from the middle Permian Lower Member of the Akasaka Limestone of central Japan, is reconstructed based on 19 specimens from the type locality. The results show that *S. akasakaensis* is characterized by a bamboo leaf-shaped shell form, an antero-posterior shell length of over 1 m, a well elevated dorsal crest and upturned wing-like valves in the anterior part of the shell.
2. Examination of previously described and additional specimens from the Funabuseyama Formation in the Neo area demonstrates that these specimens differ from those of the Akasaka Limestone in having a less elevated and shorter dorsal crest and more flattened valves in the anterior part of the shell. A new species, *Shikamaia ozakii* Asato and Kase sp. nov., is proposed for the Neo specimens.
3. The ventral gape, a slit-like opening along the shell commissure on the dorsal side, is a shell character newly identified in this study.
4. The shell of the two *Shikamaia* species is comprised of a very thin prismatic layer that is underlain by a thin layer of fine-grained calcite and a thick layer of coarse-grained calcite, all of which extend to the posterior margin of the shell. The presence of the two grained layers would have prevented the penetration of sunlight during life, which contradicts the previous hypothesis that *Shikamaia* was a photosymbiotic bivalve similar to the modern cardiid bivalve *Corculum cardissa*. However, the mode of life of alatoconchids still remains uncertain.

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