An Ancient Brachiopod with an Organic Integument from the Lower Cambrian of Mongolia

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Received June 25, 2003

Abstract—A new bivalved organism, identified as the earliest brachiopod *Zhegallina antiqua* gen. et sp. nov., is described from the Atdabanian Beds of the Dzun-Artsa locality. The inner surface of one specimen has a cast of a soft body that shows clear traces of the muscular system. The primary composition of the integument, its microstructure, and probable relationships between early brachiopods and halkieriids are discussed.

Key words: ancient brachiopods, traces of muscular system, organic integument, relationships with halkieriids, Lower Cambrian, Mongolia.

INTRODUCTION

A carbonate formation about 200 m thick exposed near Dzun-Artsa Mountain (Dzabkhan Massif, Western Mongolia) is composed of raspberry-red bedded and unbedded limestones, often clayey or containing some coarsely grained terrigeneous material. The limestone contains small biogenic buildups (bioherms), which are especially abundant in the upper part of the section. The entire series of rocks contains organic remains, predominantly algae and archaeocyatheans, on the basis of which the limestones of the Dzun-Artsa Massif are dated as the Atdabanian (Voronin *et al.*, 1983; Wood *et al.*, 1993). The upper part of the series contains a few remains of mollusks (*Obtusoconus* and *Ilsanella*), sponge spiculae, chancellorians, tommotiids, and hyolithes. One of the old brachiopod genera, *Dzunarzina* Ushatinskaya, 1993 (order Paterinida), has also been described from this section (Ushatinskaya, 1993). Apart from the above fossils, over a hundred isolated valves 1–1.5 mm in size, composed of phosphate or secondary layered silicate and externally resembling brachiopods, were found in the upper part of the section. The valves are bilaterally symmetrical, and the umbonal part is located in the posterior half of the shell. They are oval, slightly wider than they are long, and show features of hemiperipheral growth. Some valves have a shallow notch in the center of the posterior margin, while, in others, the posterior margin is almost straight or shallowly arched inside. Because both types of valves are built of the same material, have a similar outline, are of equal size, and occur in the same samples, they appear to belong to the same species. All the valves lack morphological structures typically found in brachiopods, including the earliest ones, i.e., defined umbos, areas, septa, and muscle scars. There is no certainty as to the primary composition of the valves studied. Some are composed of calcium phosphate and, sometimes, silicified. Others are composed of layered silicate (illite or chlorite), as the microanalyzer shows the presence of Mg, Al, Si, K, Fe, and very small amounts of P and Ca. Some valves are in places composed of phosphate, while other zones of the valves are built up from layered silicate. Apparently, in all cases, this composition is not primary. It is likely that these valves were dense organic covers in the living animal that were mineralized postmortem. This is supported by the fact that the valve outline and length-to-width ratio are highly variable, by the festooned or strongly curved valve margins, and the valve shape that resembles a cup. It is possible that these valves would have been considered to be sclerites of uncertain taxonomic origin, if a mineralized cast on the inner surface of one valve had not been discovered. This cast supposedly belonged to the soft body of the animal (its visceral cavity), which enclosed most of its inner organs (Pl. 2, fig. 2). The cast is slightly elevated over the surface of the valve, a rounded rhomboid in outline with a distinct bilateral symmetry, and narrows toward the anterior margin. Several pairs of symmetrical ovals are clearly seen along the lateral and anterior margins. The shape and arrangement of these ovals resemble those of muscles in the brachial valves of lingulid brachiopods, which, in the latter, also surround the visceral cavity. Supposedly, the valves discovered belonged to very early brachiopods (or even pre-brachiopods) that lacked a mineralized shell, a differentiated umbo, and areas, but had a soft body typical of early brachiopods and a small notch (a passage for the pedicle). At present, the origin and relationships of the early brachiopods are being debated (Conway Morris, 1998; Holmer, 2002), hence, the description of one of the earliest members of this group may help evaluate the pos-

sibility of links between the early brachiopods and other fossil organisms.

The stratigraphic position and sample numbers are given in accordance with Voronin et al. (1983). Collection PIN, no. 3302 is housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN). SEM photographs were produced on a CAm-SCAN-4 in PIN. Semiquantitative microprobes were performed on an Sbs-50 M NPO UNI-Expert microanalyzer. The results are shown using graphs.

SYSTEMATIC PALEONTOLOGY

Phylum Brachiopoda

Class, Order, Family incertae sedis

Genus *Zhegallina* Ushatinskaya, gen. nov.

Etymology. In honor of Elena Aleksandrovna Zhegallo, who collected and donated material described in this paper.

Type species. *Zhegallina antiqua* gen. et sp. nov.

Diagnosis. Valves small, bilaterally symmetrical, oval, slightly extended laterally, of two types: with relatively deep incision located in the middle of posterior margin and with posterior margin slightly concave, gently arched, or almost straight. Notch supposedly homologous to pedicle groove of brachiopods. Hence, valves with notch (pre-delthyrium) on posterior margin considered to be pedicle valve, while valves with straight or gently arched posterior margin considered to be brachial valve. Lateral angles rounded in all valves. Umbos not defined. Umbonal zones slightly elevated above valve surface and slightly thickened from outside. External surface in some specimens possesses thin radial striation. Concentric growth lines weakly discernible in posterior parts of valves and distinct in anterior parts.

Valve interiors without any morphological structures (areas, pedicle grooves, muscle scars, ridges). Visceral cavity of brachial valve of approximately two-thirds of valve length and half of valve width; rounded-rhomboid in outline. Visceral periphery with several pairs of symmetrical ovals along anterior and posterior margins, resembling muscular system of brachial valves of early members of Lingulida.

Species composition. Type species.

Zhegallina antiqua Ushatinskaya, sp. nov.

Plate 1, figs. 1–6; Plate 2, figs. 1–4

Etymology. From the Latin *antiquus* (antique).

Holotype. PIN, no. 3302/5108; brachial valve; western Mongolia, Dzabkhan Massif, near Dzun-Artsa Mountain; Lower Cambrian, Atdabanian Stage.

Description (Fig. 1). The valves are small, bilaterally symmetrical, oval, and slightly extended laterally, with hemiperipheral growth. Their size does not exceed 1–1.5 mm. Two types of valves are present. In type 1, a relatively deep notch is present in the middle of the posterior margin (Pl. 1, figs. 1, 2). In type 2, the posterior margin is only slightly arched inward or is almost straight (Pl. 1, figs. 3–6). The notch may be homologous to the pedicle groove. As in brachiopods, to which these valves are tentatively assigned, the valve with a notch (pre-delthyrium) is considered a pedicle valve, while valves with a straight or gently concave posterior margin are considered brachial valves. The lateral angles are rounded in all valves. Sometimes, the entire valve is thin, but there are specimens that are thin only near the posterior margin and strongly elongated near the lateral and anterior margins because of the deposition of auxiliary layers. Such valves are usually strongly convex and, in the interior view, resemble a vase with a thickened outer rim. In some valves, the lateral and anterior margins have one, two, or three gentle curvatures and, in this case, their margins are festoon-shaped (Pl. 1, fig. 6a; Pl. 2, fig. 3). The umbos in both valves are undifferentiated, but the umbonal zones are slightly raised over the remaining valve surface and slightly thickened externally because of the thin band located in the umbonal zone along the posterior margin (Pl. 1, fig. 5b). The valve's surface is covered by thin radial striae radiating from the umbonal zone and, occasionally, dichotomizing toward the anterior margin. On other valves, radial ribbing is not developed. Concentric growth lines are weakly discernible in the posterior part of the valves and distinct in the anterior half, especially if the valves are thickened anteriorly.

The interior of the overwhelming majority of the valves lacks any morphological structures. The inner surface of one specimen possesses a mineral cast, apparently of the soft body of the animal (Pl. 1, figs. 2a, 2b). The cast occupies approximately two-thirds of the valve's length and half of its width and is slightly elevated above its internal surface. The cast is a rounded rhomboid in shape, almost straight posteriorly, and narrows anteriorly. Its bilateral symmetry can be clearly seen. This appears to be a visceral cavity that contained the animal's internal organs. Several pairs of symmetrical ovals are clearly visible on the cast's periphery along the lateral and posterior margins. The shape and arrangement of these ovals resembles the muscular system in the brachial valves of lingulid brachiopods. Two pairs of posterior ovals lying near the posterior margin of the cast can be interpreted as a group of posterolateral muscles. One (or two?) pairs of ovals in the middle part are apparently casts of central muscles. Finally, a pair of anterior muscles is located next to each other anteriorly. A similar arrangement of muscles inside the brachial valves is observed in some early Lingulida. For instance, a similar muscular system structure was described in *Kyschabactella* Koneva, 1986 and in *Zhanatella* Koneva, 1986 (Pelman et al., 1992).
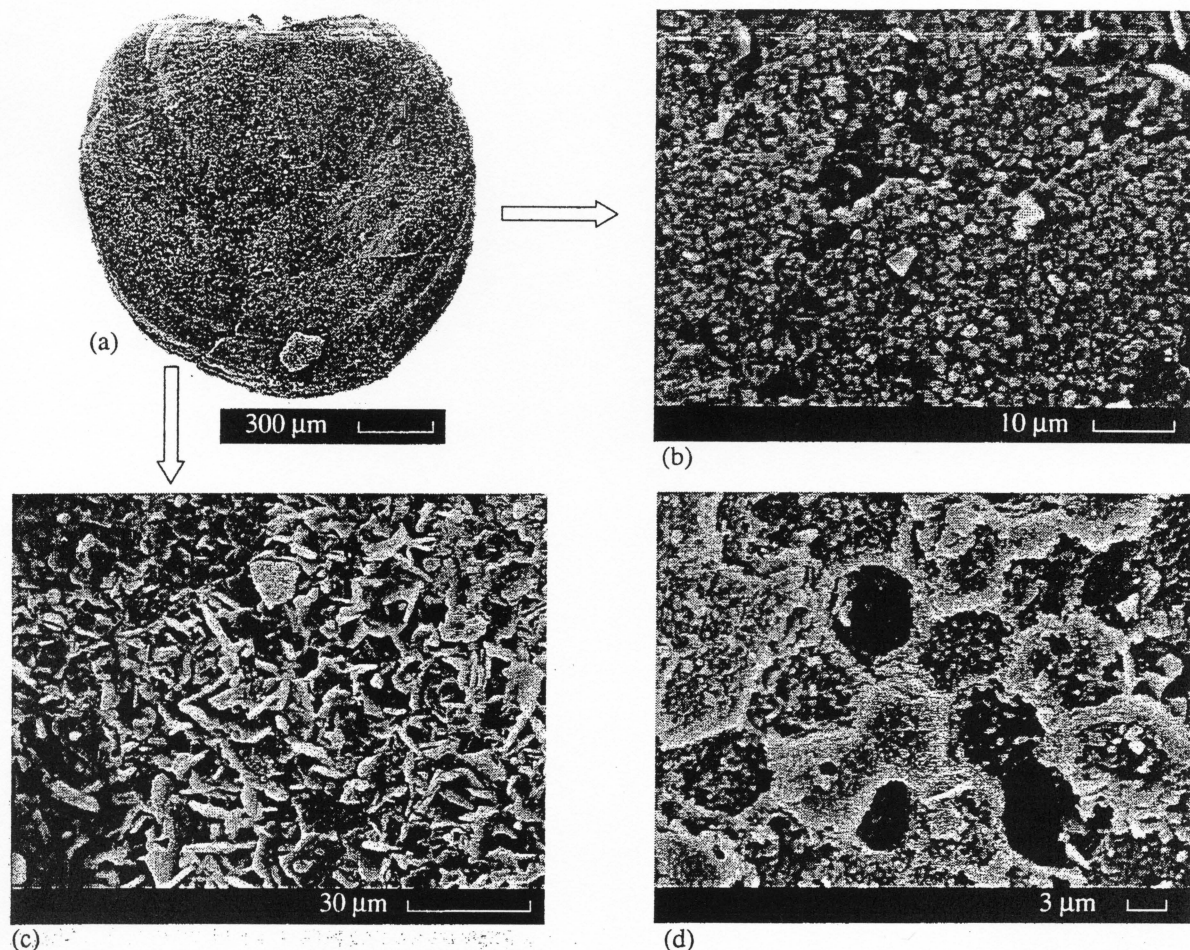
Material. Over 100 isolated valves from the type locality.

Plate 1
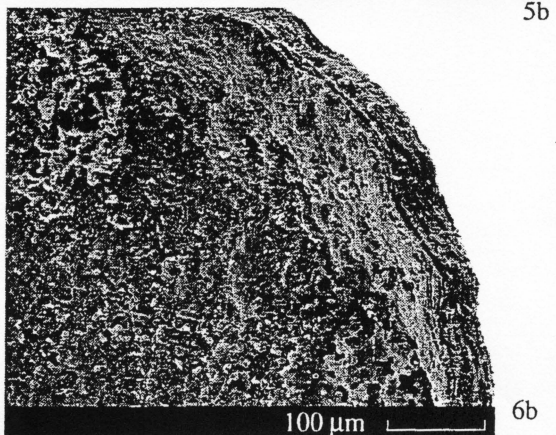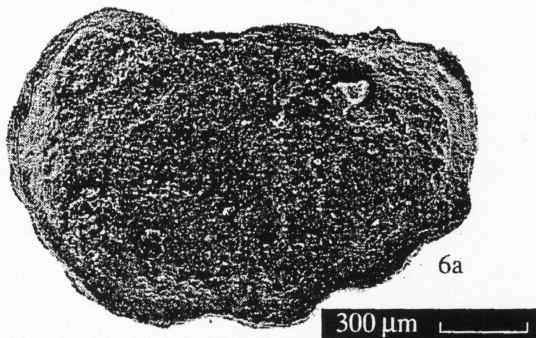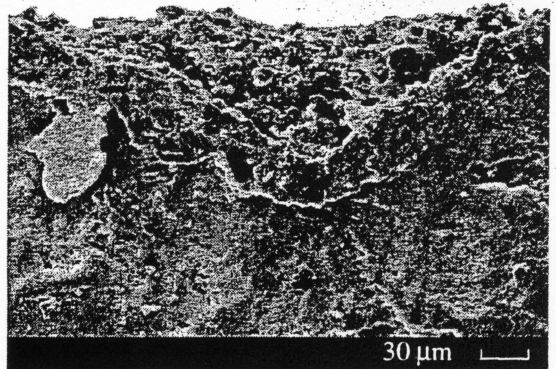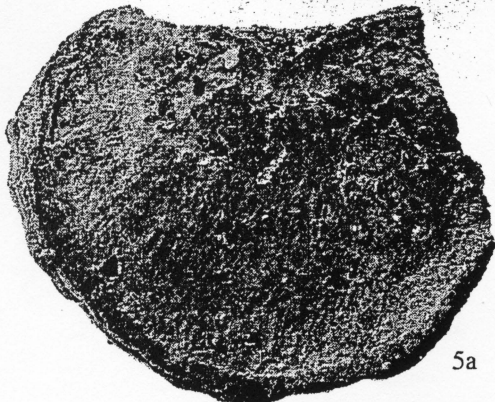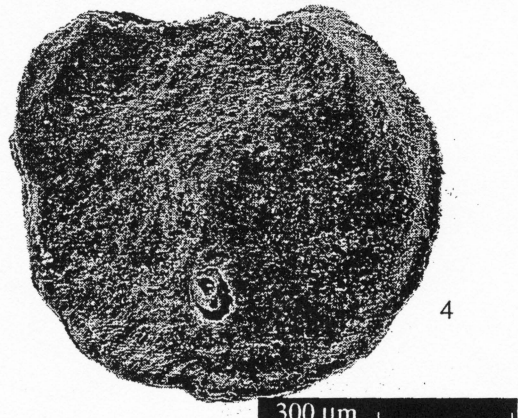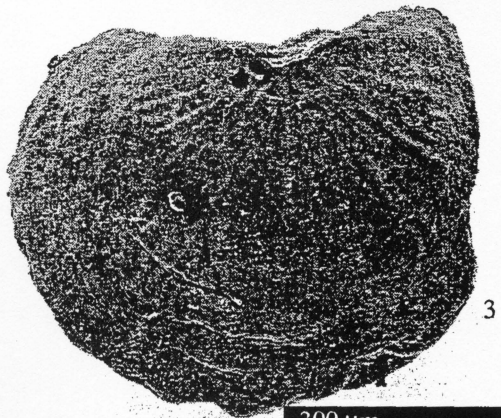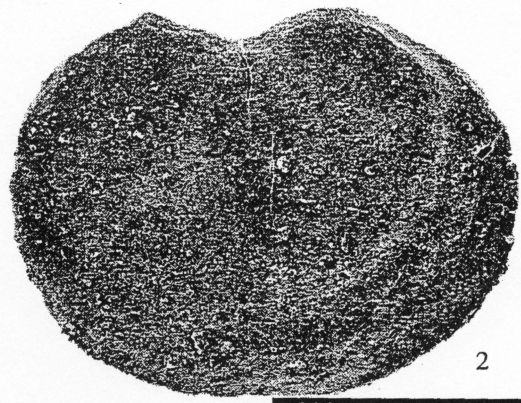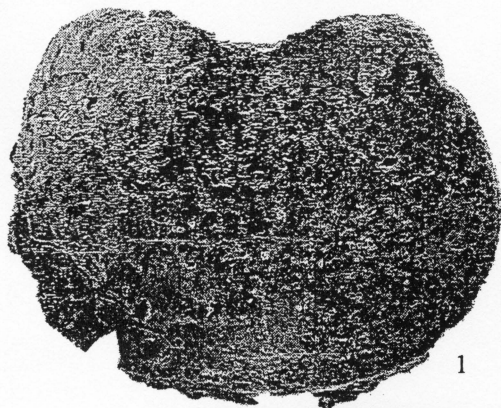
Fig. 1. *Zhegallina antiqua* sp. nov., (a–c) specimen PIN, no. 3302/5111: (a) "brachial" valve exterior; (b) fragment of the surface showing small cubical crystals composed of calcium phosphate with admixture of Mg, Al, Si, and K (see Fig. 2d); (c) fragment of the surface of the same valve with needle-shaped crystals composed of Mg, Al, Si, Fe (see Fig. 2c); and (d) specimen PIN, no. 3302/5112, fragment of the inner surface of the "brachial" valve, which show well preserved impressions of the cells of the external epithelium of the mantle.
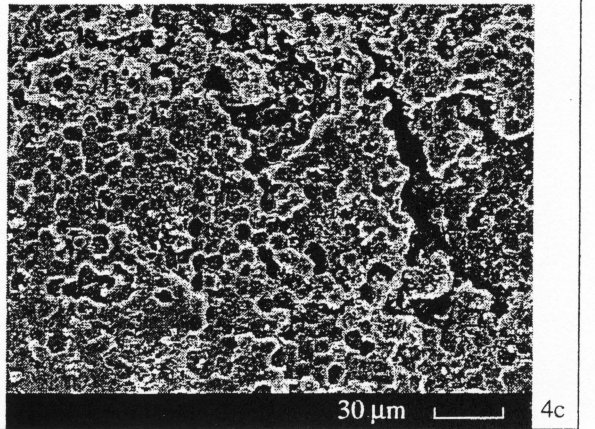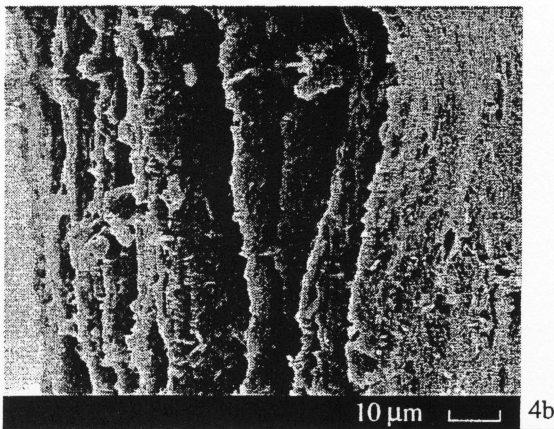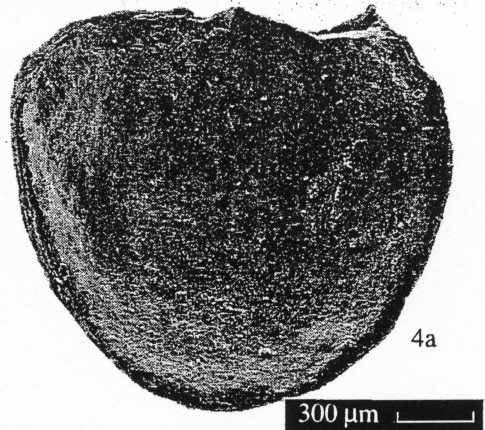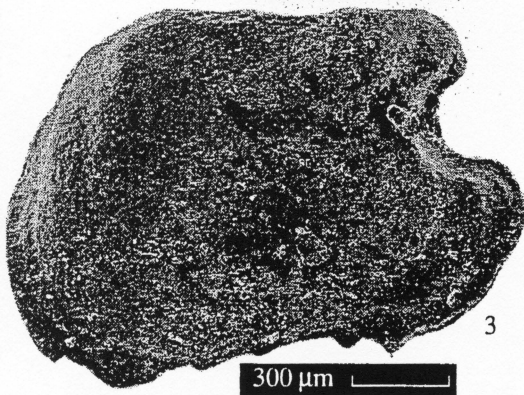
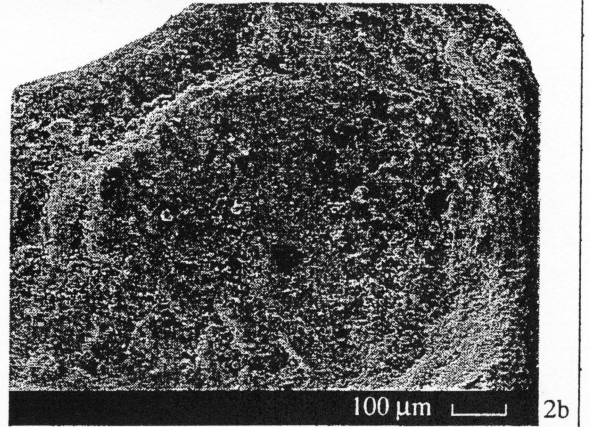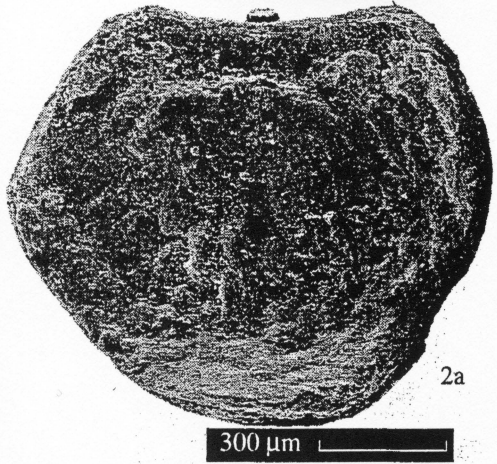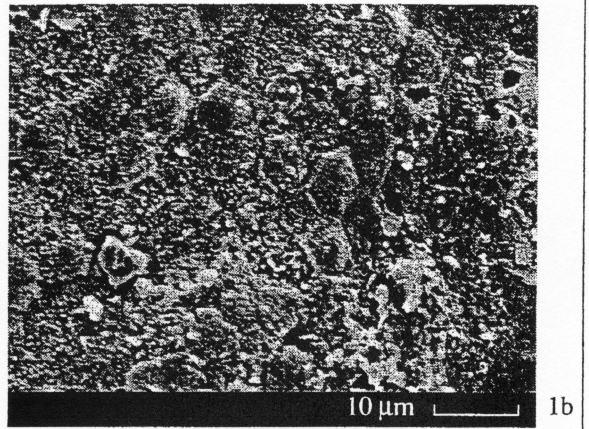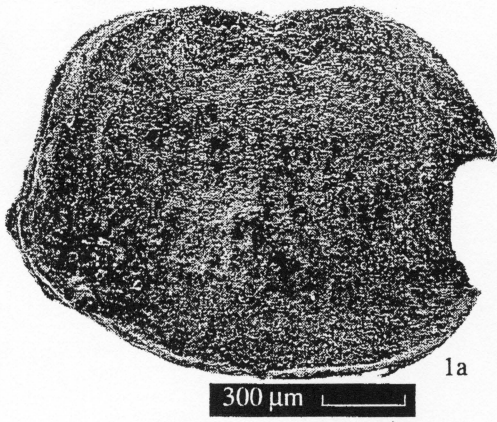## MICROSTRUCTURE AND MINERAL COMPOSITION OF THE VALVES

Microstructure. The valves are composed of numerous thin laminae, parallel to each other and to both surfaces. This is clearly seen in specimens, which are thickened toward the lateral and anterior margins (Pl. 1, fig. 6b; Pl. 2, fig. 4b). The laminae are about 2–3 μm thick. They are extended, tightly contact each other, are sometimes fused, and then diverge. Occasionally, earlier laminae project from under those formed later, and, sometimes, laminae which were deposited last overlie all those below them. The laminae often possess imprints of cells. They are not only present on the lamina covering the inner surface, but also on the deeper ones, which is seen in places where some laminae have been removed (Pl. 2, figs. 1b, 4c). The imprints of cells are also present on the outer side of the valves if the outermost layer is absent. The cells are most often preserved as imprints, but, sometimes, only the septa between them, or, in contrast, the casts of cells as convex hexagons are present. In these cases, it is seen that the cell content is composed of small, similar crystallites of calcium phosphate, which, sometimes, are

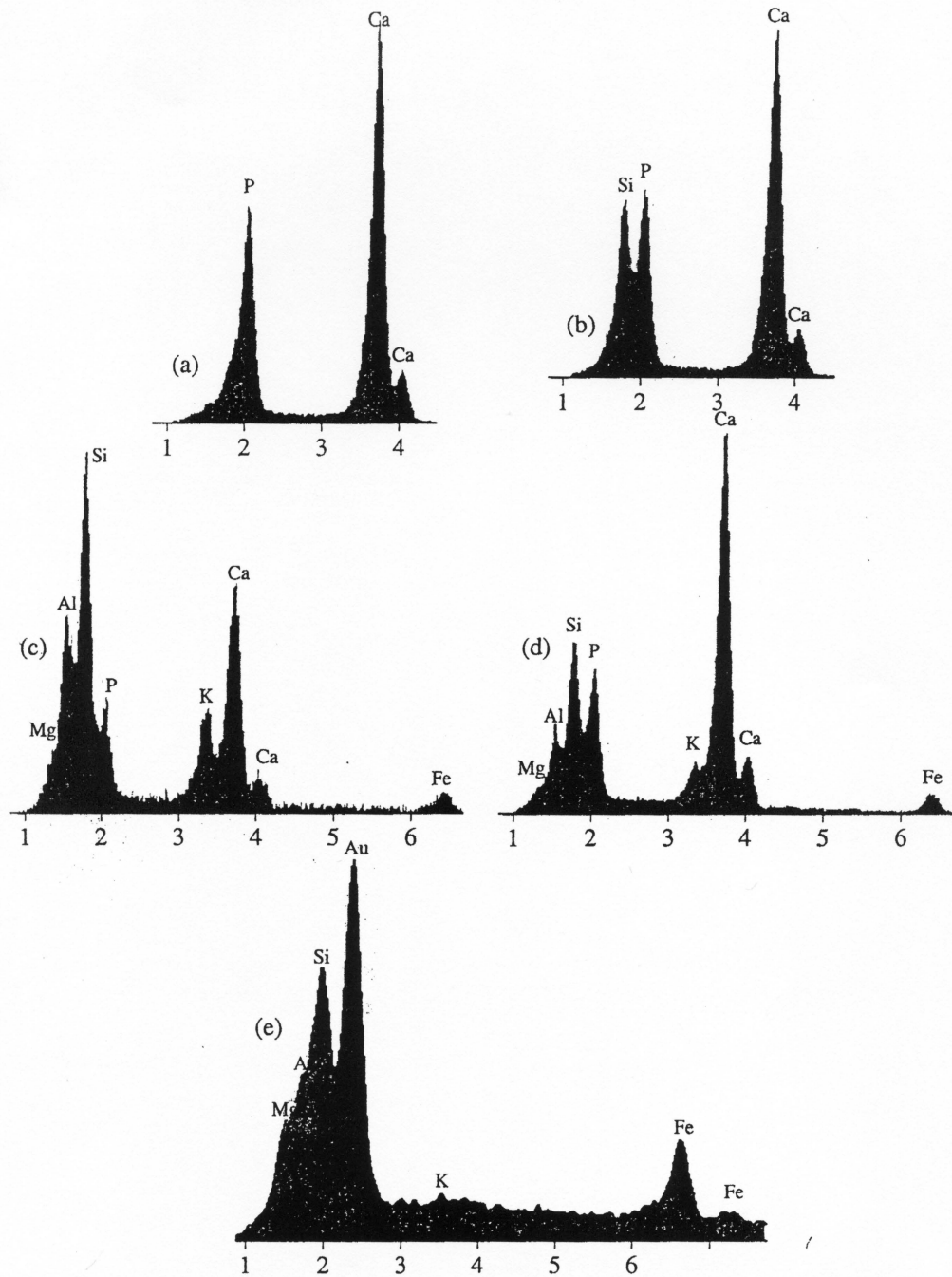Plate 2

1a

1b

2a

2b

3

4a

4b

4c

Fig. 2. *Zhegallina antiqua* sp. nov., energy-dispersion spectrum of fragments: (a) on the inner surface of the "brachial" valve with cell impressions (see Fig. 1d), specimen PIN, no. 3302/5112; (b) on the inner surface of the "pedicle" valve, specimen PIN, no. 3302/5113; (c) on the outer surface of the "brachial" valve near the umbo, showing the needle-shaped crystallites of illite, specimen PIN, no. 3302/5111; (d) on the outer surface of the "brachial" valve showing cubical crystallites of silicified calcium phosphate, specimen PIN, no. 3302/5111; and (e) the outer surface of the "pedicle" valve near the umbo showing the needle-shaped crystallites of illite, specimen PIN, no. 3302/5114.

Explanation of Plate 2

All specimens depicted come from the upper part of the section of Dzun-Artsa Mountain, western Mongolia, Dzabkhan Massif; Lower Cambrian, Atdabanian Stage.

Figs. 1–4. *Zhegallina antiqua* sp. nov.; (1) specimen PIN, no. 3302/5107: (1a) "brachial" valve interior and (1b) enlarged fragment of the inner surface with impressions of cells of external epithelium of the mantle; (2) holotype PIN, no. 3302/5108: (2a) "brachial" valve interior with a mineralized cast of the soft body and (2b) the same, enlarged; (3) specimen PIN, no. 3302/5109, brachial valve interior showing a gentle curvature of the valve near the lateral margin; and (4) specimen PIN, no. 3302/5110: (4a) "brachial" valve interior, (4b) fragment of the same specimen near the lateral margin showing lamellar microstructure of the valve, and (4c) fragment of the inner surface with the impressions of cells of external epithelium of the mantle.

dumbbell-shaped and, sometimes, cubical (Fig. 1d). The shape of the crystallites appears to depend on the mineral composition of the valves. The size of the cells does not exceed 6–8 µm.

Mineral Composition of the Valves. The valves recovered from different beds in the Dzun-Artsa section may be green, light green, or white. Sometimes, the valves are greenish outside and white inside. The anterior part of the valve may sometimes be more densely green than the posterior. The study by the LINK microanalyzer showed that the white valves are most often composed of pure calcium phosphate (Fig. 2a) or from silicified phosphate (Fig. 2b). The green valves contain Mg, Al, Si, and small quantities of K and Fe and occasionally retain small amounts of P and Ca. The green valves and thin green fragments from the same samples are most often composed of layered silicate (illite), which is usually abundant among glauconites (Fig. 2e). One valve, with a partly destroyed outer layer, displays the presence of Al, Si, P, C, and Fe (small amount), while the inner layers are composed of pure calcium phosphate. The outer surface of one valve (Fig. 1a) is in places composed of short (to 10 µm in length) and thin (1 µm thick), needle-shaped crystallites composed of Mg, Al, Si, Fe, and K (Figs. 1c, 2c). Other zones of the same valve are composed of very small cubical crystals, mainly containing Ca and P and small amounts of Mg, Al, Si, and K (Figs. 1b, 2d). It is possible that these are fragments of the partly preserved mineralized periostracum. Such elementary and mineral compositions suggest postmortem mineralization of a primarily organic integument. Near the inner surface, in the proximity of the soft body, the decay of this body resulted in the release of free phosphorus, which caused phosphatization of the inner laminae, sometimes simultaneously with silicification. The external surface, which was also organic in the living organism and contacted the outer medium enriched by ions of clay minerals, was the place of formation of the layered clay mineral (illite). Only the denser periostracum, apparently containing chitin, was replaced by calcium phosphate. The hypothesis of a primarily organic composition is supported by the occasional valves that weakly curve on the margins (Pl. 1, fig. 6a; Pl. 2, fig. 3). If the valves were mineral in the living organism, they would have broken, as always happens even in very thin mineral brachiopod shells, rather than being bent.

DISCUSSION

The valves described show some characters that allow placing them into the phylum Brachiopoda. These animals were most likely bivalved. The outlines of the so-called pedicle and the so-called brachial valves corresponded to each other, and the valves and the soft body were bilaterally symmetrical. The visceral cavity occupied the posterior part of the shell. There was a notch in the so-called pedicle valve, which may have provided passage for the pedicle, while the mus-

cles were arranged symmetrically. The soft body was enclosed in the mantle, which is indicated by the imprints of uniform cells over the entire inner surface of the valves. The valves were composed of thin laminae, which were parallel to each other and deposited by the outer mantle layer. In contrast to all known brachiopods, including the earliest taxa, the valves did not have delineated umbos and areas and were apparently organic rather than mineral in composition. It is most likely that the organic matter also contained chitin, which aided postmortem mineralization of the valves. Thus, the animal was soft-bodied, if we consider only primarily mineral shells to be skeletal. The organic nature of the integument also explains the absence of umbos and areas, which are usually used for firmer attachment of shells to the bottom and can develop as hard structures only in mineralized valves. The absence of noticeable muscle scars on the inner surface of the valves of *Zhegallina antiqua* is also explained by the original organic composition. These valves cannot be assigned to any known brachiopod order. Judging from the muscle arrangement, this group, with its organic integument, is most likely ancestral to brachiopods with a phosphate shell.

The discovery of the imprint of *Halkieria evangelista*, which clearly shows traces of anterior and posterior valves very much resembling those of brachiopods, in the Botomian (Lower Cambrian) of Greenland in the early 1990s sparked a debate over whether halkieriids are the immediate ancestors of brachiopods (Conway Morris and Peel, 1995; Conway Morris, 1998; Williams and Holmer, 2002; Holmer *et al.*, 2002). Conway Morris and Peel (1995) suggested that halkieriids, which floated above the bottom of the Cambrian seas, were eventually able to fold in such a way that one valve was above the other, whereas other halkieriid sclerites transformed into chaetae. Furthermore, through a series of successive gradual transformations, halkieriids gave rise to the phylum Brachiopoda.

Later, the genus *Micrina* was described from the Late Cambrian beds of Australia, and its microstructure was described in detail (Ushatinskaya, 2002, Williams and Holmer, 2002). Both papers suggested that the sellate and mitral sclerites of *Micrina*, morphologically speaking, very closely resemble the anterior and posterior valves of *Halkieria evangelista* and that *Micrina* is the sister group for halkieriids. Williams and Holmer developed the hypothesis of Conway Morris and Peel that halkieriids are ancestral to brachiopods. They recognized nine major transformations that could have led to the emergence of brachiopods from a halkieriid ancestor. These included acceleration of the mixoperipheral growth of the valves in halkieriids, especially in the anterior (dorsal) half; the development of the lophophore; the development of the mantle cavity by the refitting of the anterior valve margins to conform each other; the regrouping of the muscular system; and the formation of the pedicle as an attachment organ. This hypothesis runs into several difficulties. Study of

the members of the genus *Micrina* from southern Australia has shown that the umbonal part of the mitral sclerite, which is, indeed, very similar to that in early brachiopods (paterinids), is not distinctly bilaterally symmetrical, its umbo being oblique (Ushatinskaya, 2002, pl. I, figs. 1, 7, 11). Two tooth-shaped processes, which are present in the mitral sclerite in *Micrina*, cannot be homologous to brachiopod teeth. They do not grow on the sides of the delthyrium, but are raised from the bottom of the sclerite, and their arrangement and size do not show clear symmetry. They are not solid, as in brachiopods, but are composed of hollow tubes, extending along these structures parallel to their long axes. Their growth was not a result of thickening of the shell matrix, but of thickening along the long axis because of an increase in the number of tubes. It is possible that, in the living animal, these tubes were grouped bunches of epithelial outgrowths by means of which the organic-mineral mitral sclerite was attached to the soft body of the halkieriid animal. The anterior (sellate) sclerite of *Micrina* also lacks strict bilateral symmetry, while the difference between the outline of the sellate and mitral sclerite is very large (ibid., pl. I, figs. 15–18). In addition, both the mitral and sellate sclerites had umbos and posterior flattened zones, similar to the delthoidal area, that were only superficially similar to brachiopod areas, especially in the sellate sclerite. The material examined in this paper shows that the earliest brachiopods with nonmineralized integuments did not have well-defined umbos and palintrope. They acquired the shell shape typical of skeletal brachiopods only along with mineralization of their valves.

The similarity of the chitinous chaetae in brachiopods, annelids, and possible halkieriids is very supportive of the hypothesis that brachiopods originated from halkieriids. Based on this, Conway Morris and Peel and Williams *et al.* derive the chaetae in polychaetes and brachiopods from the sclerites of halkieriids, which they consider to be an apomorphy. However, the chaetae in the gizzard of some bryozoans, chaetognaths, and pogonophores are also similar. In addition to the presence of chaetae, brachiopods are close to bryozoans and chaetognaths, along with phoronid, in such important characters as radial egg cleavage, enterocoel derivation of the coelom, and reduction of the aboral organ in metamorphosis (Malakhov and Galkin, 1998). At the same time, polychaetes have a spiral egg cleavage, while their mesoderm develops through teloblasts, and the esophageal ganglion has a primary origin. Such significant differences in the embryonic development of brachiopods and annelids invalidate the hypothesis that the annelids (and, hence, halkieriids, which are similar to polychaetes in a number of morphological features) are the most probable ancestor of brachiopods (Conway Morris, 1998).

Thus, the Atdabanian of Mongolia contains the remains of organisms that can be considered the earliest brachiopods. They did not yet have a mineralized skeleton, but possessed an organic integument and a soft body that, morphologically, most closely resemble those of brachiopods with a phosphate shell of the class Lingulata.

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