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The Ontogeny of the Late Permian Terebratulids (Brachiopoda) *Gruntelasma* Smirnova, *Grigorjevaelasma* Smirnova, and *Campbellelasma* Smirnova and Their Taxonomic Position

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Abstract—A specific type of ontogenetic change combining elements of dielasmoid and angustothyridid stages of brachidium development is established for the Late Permian genera *Gruntelasma* Smirnova, 2004, *Grigorjevaelasma* Smirnova, 2004, and *Campbellelasma* Smirnova, 2004 from the Russian Platform. On this basis, these genera are assigned to the superfamily Compositelasmatoidea Smirnova, family Compositelasmatidae.

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Key words: Russian Platform, Late Permian, Early Kazanian, Zechstein, Sok River.

INTRODUCTION

This paper continues a series of papers on the Late Permian (Lower Kazanian) terebratulids from the east of the Russian Platform. The abundance of well-preserved small shells of different ages contributed to the detailed ontogenetic investigations of the cardinalia and brachidium. The postembryonic development of the Late Permian terebratulids is poorly understood. Dagis

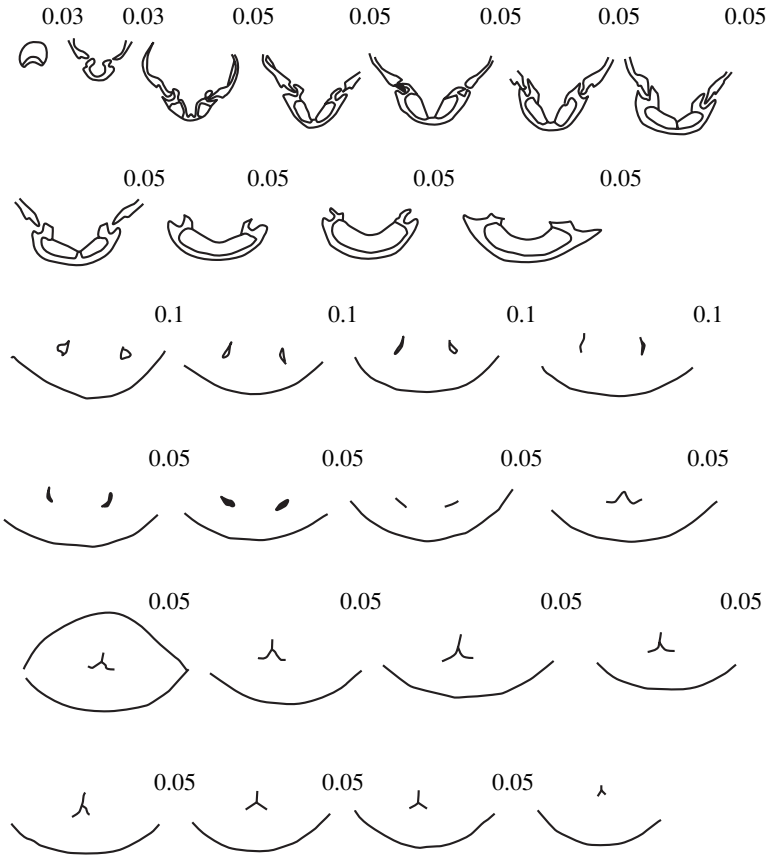

Fig. 1. *Gruntelasma bajtuganensis* Smirnova, 2004; specimen PIN, no. 4898/8, serial sections through a 3.8-mm-long shell; figures indicate distances between the sections in mm.

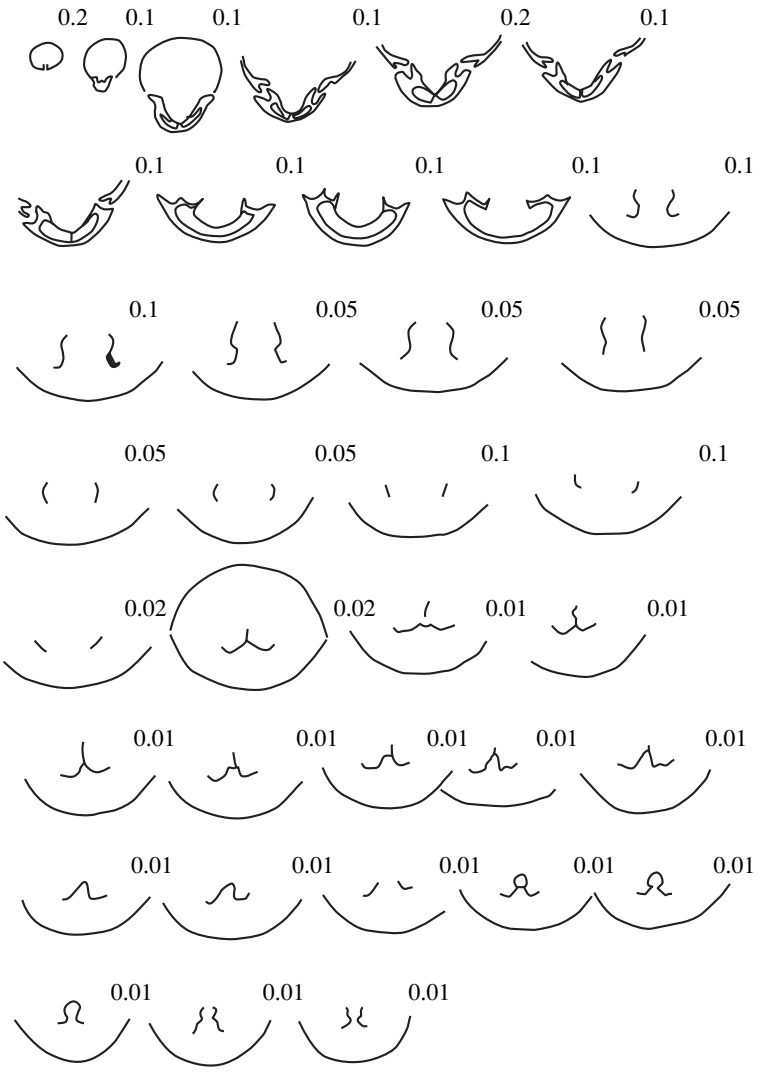

Fig. 2. *Gruntelasma bajtuganensis* Smirnova, 2004; specimen PIN, no. 4898/9, serial sections through a 6.3-mm-long shell; figures indicate distances between the sections in mm.

(1968, 1972) described developmental changes of *Dielasma elongata* from the Zechstein of Thuringia. Simple development of the loop without secondary elements was revealed. The centronelloid and mutationelliform stages were found to be based on a single vertical plate. Dagis named this type of development dielasmoid. The angustothyridid type of loop development is characterized by the presence of secondary elements, ontogenetic modifications of which lead to the formation of a triangular loop.

In the present paper, the developmental stages of *Gruntelasma* Smirnova, 2004, *Grigorjevaelasma* Smirnova, 2004 and *Campbellelasma* Smirnova, 2004 are studied. Based on the morphology of the adult shells, these genera were assigned to the family Dielasmatidae Schuchert, 1913 (Smirnova, 2004; Smirnova *et al.*, 2004). The study of successive developmental stages revealed that this type of ontogeny has a specific feature: simultaneous combination of elements of dielasmoid and angustothyridid types of brachidium development at the early developmental stages. After the early stages are completed, only one of these types (dielasmoid or angustothyridid) remains in ontogeny. The described type of development is called compositelasmoid from the genus *Compositelasma* Smirnova, 2006. The presence of the compositelasmoid type of development in these genera is the reason for assigning them to the family Compositelasmatidae.

Until recently, all Permian terebratulids from the eastern Russian Platform were referred to *Dielasma* Schuchert, 1913 (Netschajew, 1894, 1911). Grigor'eva (1967) discovered *Beecheria* Hall et Clarke, 1893 and believed it to be widely distributed in the Lower Kazanian. For lack of the data on the inner structures of the majority of terebratulids and well-pronounced homeomorphy, the taxonomic composition of the Late Per-

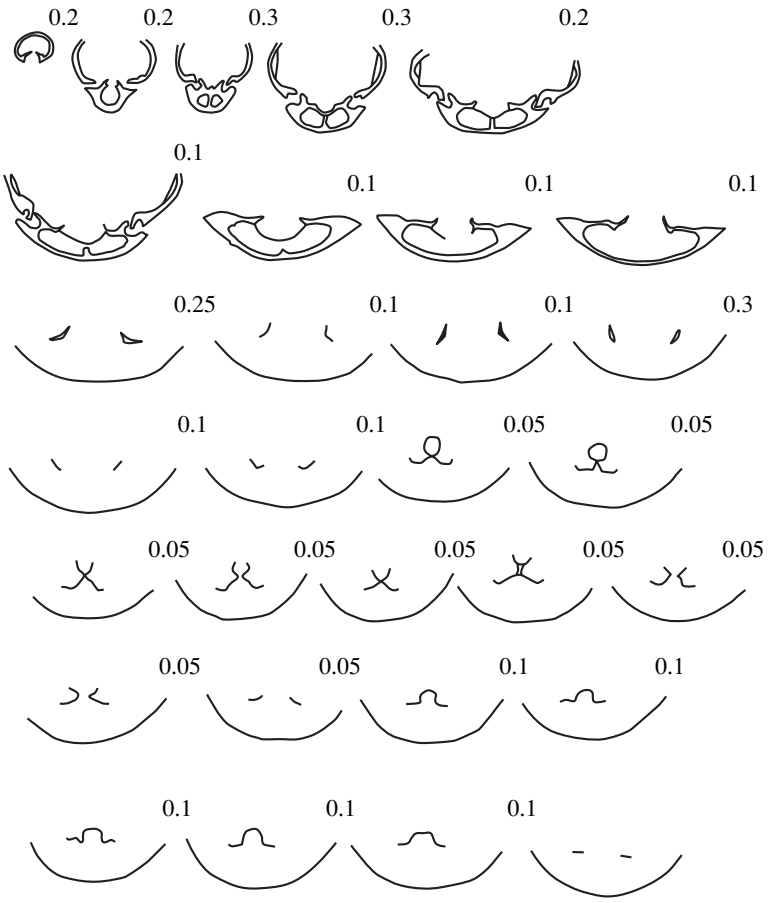

Fig. 3. *Gruntelasma bajtuganensis* Smirnova, 2004; specimen PIN, no. 4898/10, serial sections through a 7.5-mm-long shell; figures indicate distances between the sections in mm.

mian terebratulids was considered to be quite poor. The study of the shell interior of adult specimens revealed new species and genera (Smirnova, 2004a, 2004b; Smirnova *et al.*, 2004; Smirnova, 2006). The analysis of the ontogenetic changes revealed a specific type of development that is known only for the Late Permian terebratulids of the Russian Platform.

MATERIAL

The material was collected in the Samara Region, basin of the Sok River.

The collection is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN), collection no. 4898.

DISCUSSION

The developmental stages were studied in detail by cross sectioning followed by reconstruction of the inner structures, and are represented in the present paper. This method was applied to the type species of the genera *Gruntelasma bajtuganensis, Grigorjevaelasma rossicum*, and *Campbellelasma variiforme*.

Ontogenetic stages of Gruntelasma bajtuganensis. A 3.8-mm-long shell has a small pedicle collar and short dental plates pressed to the shell wall (Figs. 1, 10a). The teeth are short and enter the dental sockets obliquely. The complementary denticle is present. The inner socket ridges are high and strongly curved. The outer hinge plates are narrow. The inner hinge plates separately join the valve floor in the umbonal region; anteriorly, they are supported by the short septum and then became free. The crural bases have small ventral and dorsal tips. The crural processes are short. The first ventral vertical plate is connected with the ventrally curved domelike brachidium branches. This stage corresponds to the early mutationelliform stage of the dielasmoid type of development. The brachidium length is about two-thirds of the dorsal valve length.

A 6.3-mm-long shell lacks dental plates and pedicle collar (Figs. 2, 10b). The teeth are narrow and have complementary denticles. The inner socket ridges are steeply inclined. The outer hinge plates are short and poorly developed in the cardinalia relief. The inner hinge plates are connected to the short septum and are free anteriorly. The crural bases have well-pronounced ventral and dorsal tips. The crural processes are repre-

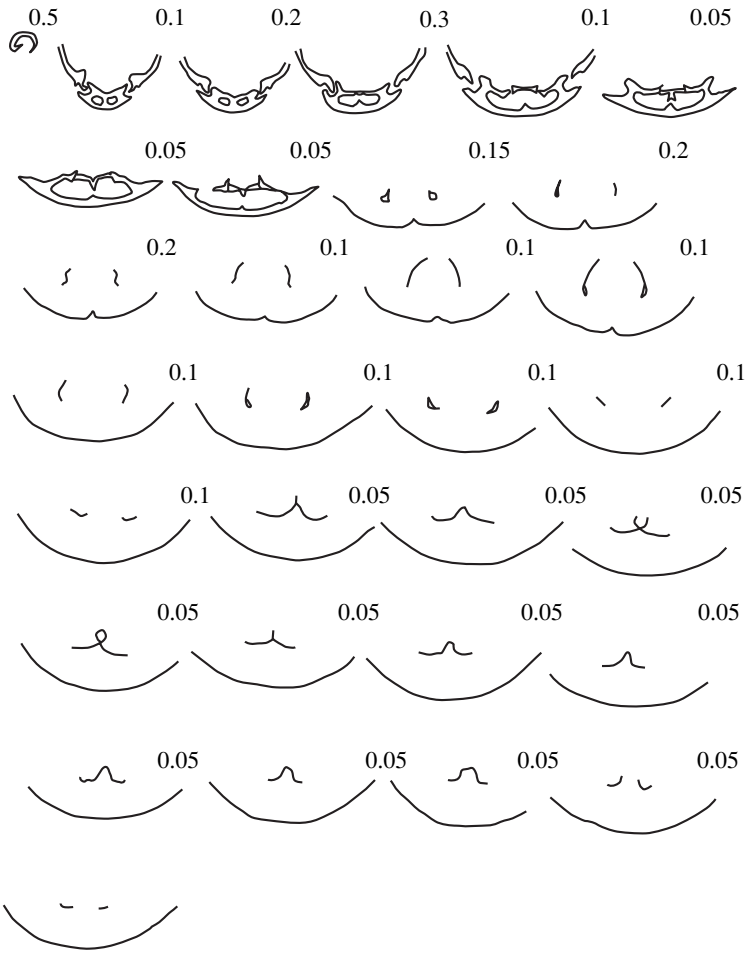

Fig. 4. *Grigorjevaelasma rossicum* Smirnova, 2004; specimen PIN, no. 4898/52, serial sections through a 6.1-mm-long shell; figures indicate distances between the sections in mm.

sented by wide, S-shaped, and curved plates. The brachidium branches are narrow. The mutationelliform stage is well-pronounced and is characterized by the first ventral vertical plate being clearly defined and brachidium with a deep ventral curve at the junction with the plate. Anteriorly, the first ventral vertical plate reduces; the brachidium branches first remain domelike and then diverge in the short interval. The anterior tip of brachidium bears secondary elements, the modification of which gives rise to the stage with a well-formed hood. The dorsal wall of the hood is partly reduced, that corresponds to the early dictiothyridid stage of the angustothyridid type of brachidium development.

A 7.5-mm-long shell has a small pedicle collar and short dental plates located close to the valve wall (Figs. 3, 10c). The teeth have a well-pronounced denticle. The outer hinge plates are horizontal and are separated in the relief from the inner socket ridges. The inner hinge plates are supported by the septum posteriorly and are free in the anterior part of the cardinalia. The crural bases have well-pronounced dorsal tips. The crural processes are short. The brachidium is in a stage of transition from the late campagiform stage to the early dictiothyridid stage. The hood is well developed, has the dorsal wall partly resorbed, and is connected with the descending branches of brachidium. The middle part of the transverse band of the loop follows the shape the hood. The loop length is about one-half of the dorsal valve length. The adult loop forms when the shell is about 10 mm long. The average length of the adult shell is 14–15.8 mm. The brachidium develops on the basis of the secondary elements. The elements of the dielasmoid type that have been described in smaller shells are absent.

Ontogenetic stages of Grigorjevaelasma rossicum. Two developmental stages that feature both the dielasmoid and angustothyridid types were revealed.

A 6.1-mm-long shell clearly shows a fragment of a pedicle collar (Figs. 4, 10d). The dental plates are absent. The outer hinge plates are separated in the relief from the inner socket ridges. The inner hinge plate is supported by the septum in the umbonal region and is free anteriorly, where it curves to form an angle and has

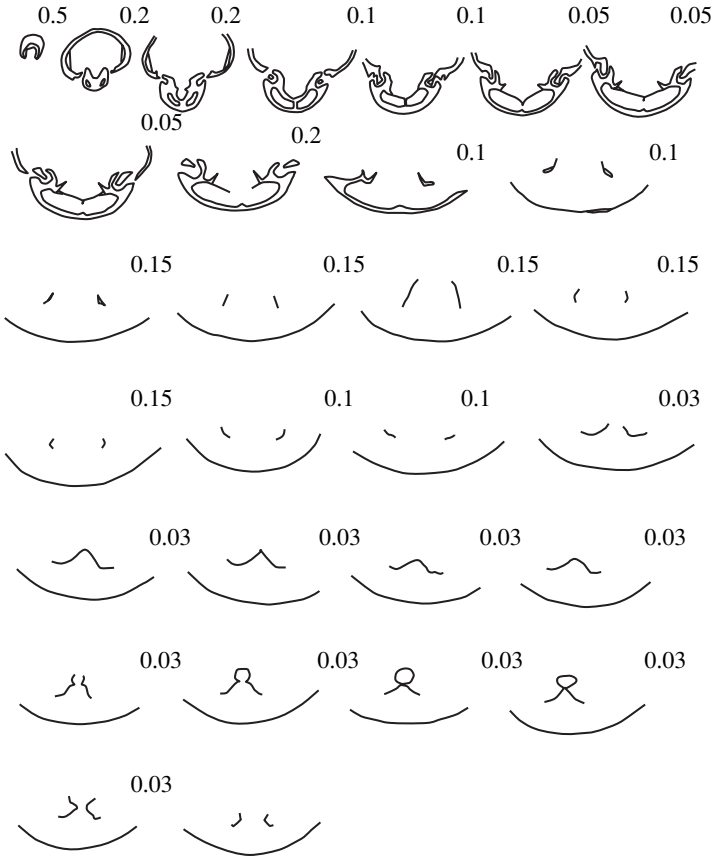

Fig. 5. *Grigorjevaelasma rossicum* Smirnova, 2004; specimen PIN, no. 4898/53, serial sections through a 6.4-mm-long shell; figures indicate distances between the sections in mm.

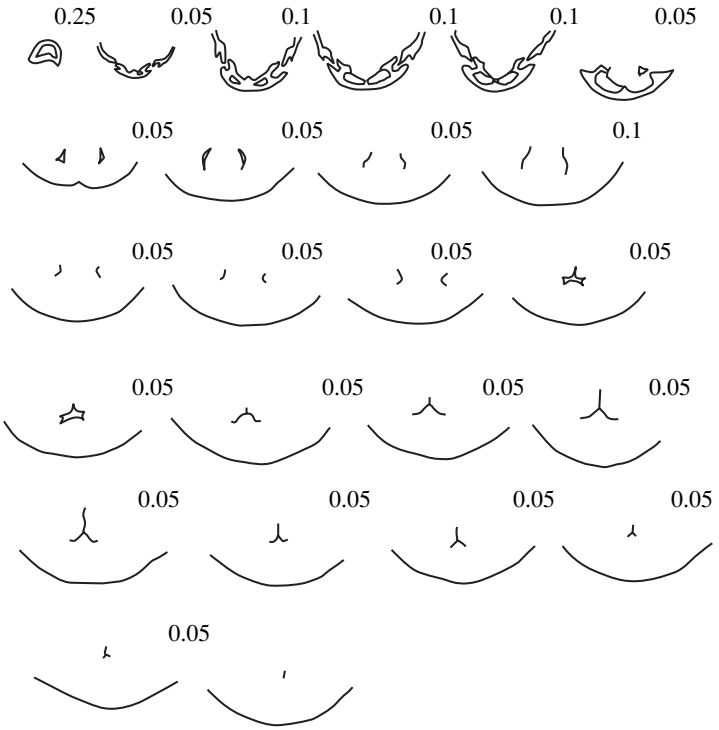

Fig. 6. *Campbellelasma variiforme* Smirnova, 2004; specimen PIN, no. 4898/1716, serial sections through a 3.0-mm-long shell; figures indicate distances between the sections in mm.

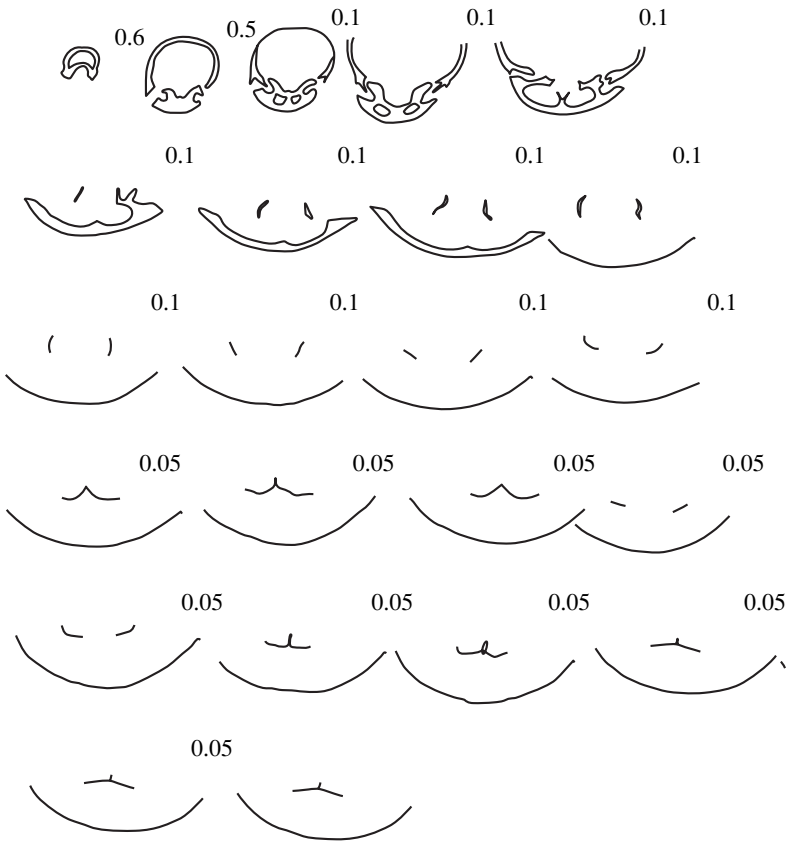

Fig. 7. *Campbellelasma variiforme* Smirnova, 2004; specimen PIN, no. 4898/1718, serial sections through a 4.0-mm-long shell; figures indicate distances between the sections in mm.

a small plate hanging over the septum. The crural bases have pointed ventral tips that are directed almost perpendicular to the outer hinge plates. The crural processes are wide. The brachidium branches are narrow. Remains of the short mutationelliform stage have been preserved and are represented by a low first ventral vertical plate that is typical for the dielasmoid type of brachidium development. The secondary elements consist of a thin hood located at the junction of the descending branches; this corresponds to the early campagiform stage of the angustothyridid type of development. The transverse band of the brachidium is strongly curved and trapezoidal. The brachidium length is about one-half of the dorsal valve length.

A 6.4-mm-long shell closely resembles the 6.1-mm-long shell in the main features of cardinalia (Figs. 5, 10e) but differs in the appearance of the dental plates pressed to the valve wall, higher crural bases, and strongly curved inner socket ridges. In the brachidium structure, it differs in the absence of the first ventral vertical plate, which had been reduced toward this developmental stage. The secondary elements consist of a large hood, a feature that corresponds to the campagiform stage of the angustothyridid type of development. The adult loop appears when the shell is about 10 mm long. The average length of the adult shell is 15–16.7 mm.

Ontogenetic stages of Campbellelasma variiforme. 3.0–3.8 mm long shells have a pedicle collar (Figs. 6, 10f). The teeth enter the sockets almost vertical. The complementary denticle is present. The dental plates are absent. The outer hinge plate is wide. The inner hinge plate is supported by the euseptoid. The crural bases have ventral and dorsal tips. The crural processes are wide. The brachidium branches are short and concave toward the shell lateral sides. The brachidium is dielasmoid, a feature that corresponds to the mutationelliform stage of development. The first ventral vertical plate is high and is supported by the fused brachidium branches. The branches are strongly curved ventrally at the junction with the vertical plate. The secondary elements of brachidium are absent. The brachidium length is about two-thirds of the dorsal valve length.

4.0–4.6 mm long shells have the same cardinalia as the 3.0–3.8 mm long shells. The 4.0 mm long shell shows remains of a well-pronounced short mutationelliform stage with a low ventral vertical plate. The descending branches first differentiate anteriorly and then connect to form a horizontal platform. In the middle of the platform, a second ventral vertical plate forms

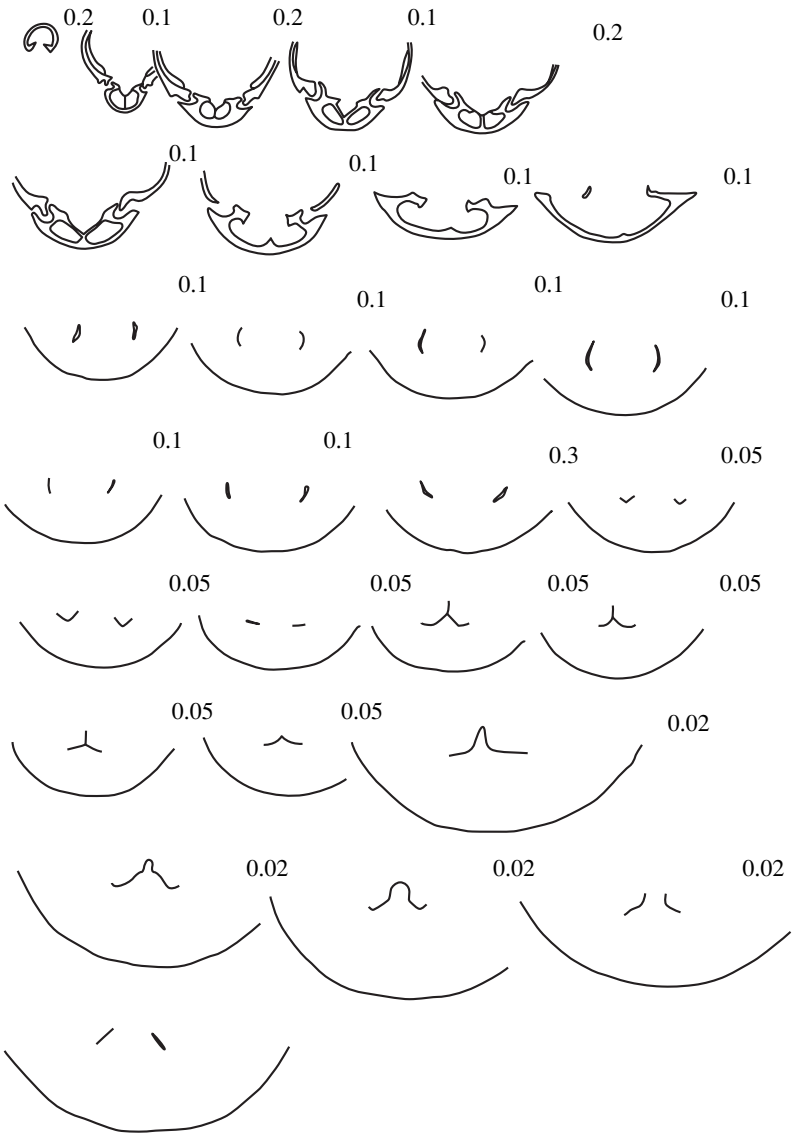

Fig. 8. *Campbellelasma variiforme* Smirnova, 2004; specimen PIN, no. 4898/1720, serial sections through a 5.0-mm-long shell; figures indicate distances between the sections in mm.

to provide abase for the development of the secondary elements of brachidium. The brachidium length is about two-thirds of the dorsal valve length.

The mutationelliform stage in the 4.6 mm long shell is characterized by a high ventral vertical plate and fused domelike-curved descending brachidium branches (Figs. 7, 10g). The descending branches converge anteriorly but then they connect to form a single platform with a horizontal surface in the middle. In the middle of the platform, closer to the anterior margin, secondary elements form. They consist of a second ventral vertical plate. The brachidium length is about two-thirds of the dorsal valve length.

In the 5.0–5.2 mm long shells, dental plates appear (Figs. 8, 10h). They are pressed to the shell wall. The pedicle collar is present. The teeth have a denticle and enter the sockets at a wide angle. The outer hinge plate is narrow. The inner hinge plate is supported by the septum and euseptoidum. The crural bases have short dorsal and elongated ventral tips. The brachidium branches are narrow. The first ventral vertical plate is connected with the V-shaped, curved, fused descending branches, a feature that corresponds to the mutationelliform stage of the dielasmoid type of loop development. In the anterior part of brachidium, the plate begins to split and the transverse band of the loop begins to form. The second ventral vertical plate, characteristic of early developmental stages, disappears in ontogeny, and the development of the brachidium follows the pattern of the dielasmoid type.

The 6.1-mm-long shell differs from the previous stage in the cardinalia structure: the dental plates are

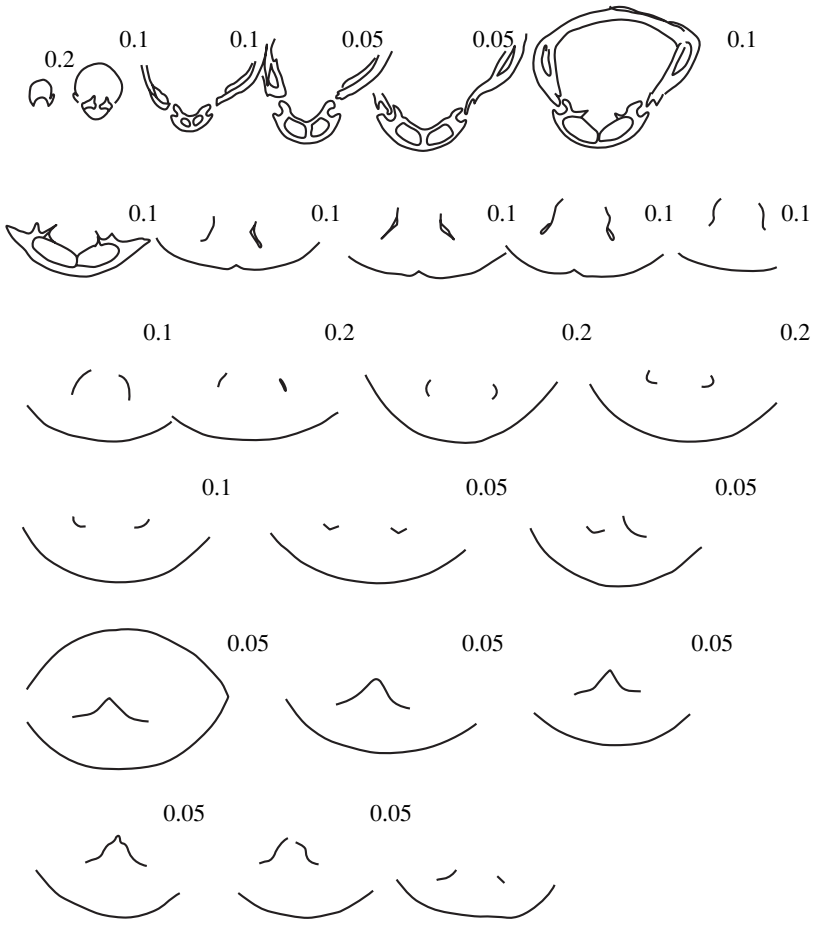

Fig. 9. *Campbellelasma variiforme* Smirnova, 2004; specimen PIN, no. 4898/1722, serial sections through a 6.1-mm-long shell; figures indicate distances between the sections in mm.

better pronounced, the inner hinge plates are supported only by the septum, and the ventral tips of the crural bases are high (Figs. 9, 10i). The loop is narrow, triangular, and resembles a dielasmoid loop. The transverse band of the loop retains some features of the mutationelliform stage: it is V-shaped in cross section and has horizontal lateral sides. The loop length is about one-half of the dorsal valve length. The adult loop appears in the shell with length about 12 mm. The average length of the adult shell is 18.0–19.6 mm.

CONCLUSIONS

Late Permian Terebratulida is one of the few groups of fossil animals that survived the global crisis at the Paleozoic–Mesozoic boundary. The study of the vast material from the eastern Russian Platform revealed a considerable diversity of taxonomic composition and complicated modifications of the brachidium in ontogeny that were previously unknown in the order Terebratulida. The compositelasmoid type of brachidium development was established for *Compositelasma evolutus* Smirnova, 2005. The study of developmental stages of *Gruntelasma bajtuganensis, Grigorjevaelasma rossicum*, and *Campbellelasma variiforme* revealed the same type of ontogeny. On this basis, *Gruntelasma, Grigorjevaelasma,* and *Campbellelasma* were assigned to the family Compositelasmatidae. The juvenile stages of these genera combine features of both the dielasmoid and angustothyridid types of development. In *Gruntelasma* and *Grigorjevaelasma*, the features of dielasmoid type of development disappear after the early stages, and only elements of the angustothyridid type persist throughout the later stages. When the shell reaches about one-third of the adult shell length, the elements of the angustothyridid type disappear. *Campbellelasma* is characterized by the loss of angustothyridid type of brachidium development during early stages, when the shell length is about one-third of the adult shell, and by the persistence of the dielasmoid type throughout the later stages. The dielasmoid type of development, which is widespread and deeply rooted in the history of Permian terebratulids, proved to be more persistent and became firmly established at the later stages. In all cases under consideration, the adult

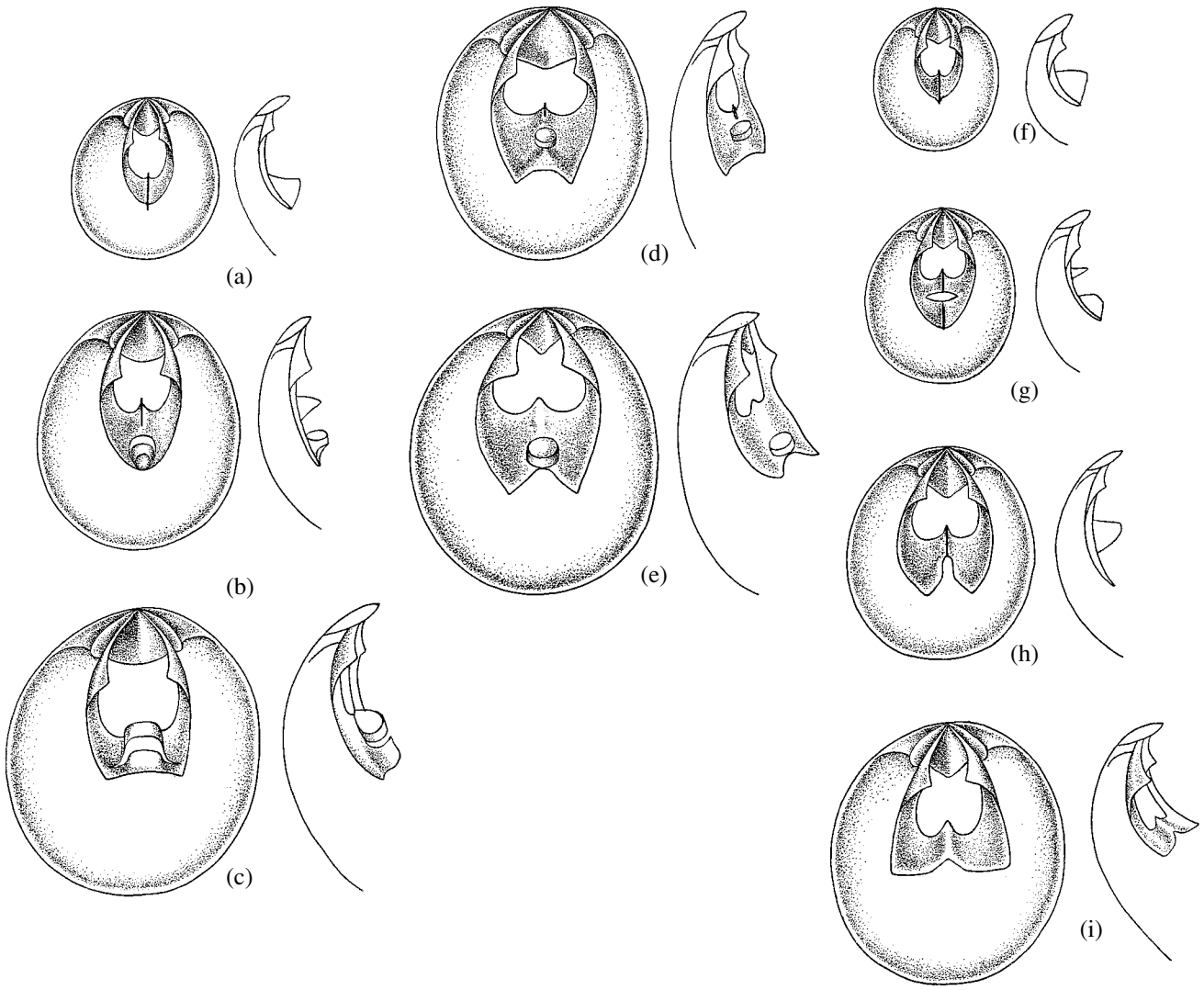

Fig. 10. Reconstruction of the shell interior: (a)–(c) *Gruntelasma bajtuganensis* Smirnova, 2004, specimens with a length of (a) 3.8 mm, (b) 6.3 mm, and (c) 7.5 mm; (d) and (e) *Grigorjevaelasma rossicum* Smirnova, 2004; specimens with a length of (d) 6.1 mm and (e) 6.4 mm; (f)–(i) *Campbellelasma variiforme* Smirnova, 2004, specimens with a length of (f) 3.0 mm, (g) 4.0 mm, (h) 5.0 mm, and (i) 6.1 mm.

brachidium formed when the shell was about two-thirds of the adult shell length.

In terebratulids, the loss of the early stages of postembryonic development of brachidium as a result of tachygenesis was mentioned by Thomson (1927). Dagis (1968) paid special attention to this phenomenon. Comparison of Dagis' data on the Triassic terebratulids with our results on the Late Permian terebratulids suggests a considerable acceleration of the formation of the adult loop in geological history. In the Late Permian terebratulids, the ratio of the length of a matured adult loop to that of an adult shell is about 0.7. According to Dagis, in the Triassic terebratulids this coefficient is about 0.3.

Different elements of cardinalia appear at different times in ontogeny. When the shell is 1–2 mm long, teeth and inner hinge plates are the first to form. The dental plates appear late. When shells are 3–5 mm long, they are poorly differentiated and usually closely pressed to the shell wall. Well-developed dental plates appear when the shell length is about one-third of the adult shell length.

It is obvious that the first attempts to create more advanced ontogenetic modifications through the appearance of secondary elements typical for the Mesozoic terebratulids took place in the Boreal paleozoogeographic region. It is hard to determine whether or not the direct descendants of these groups existed in the Mesozoic. It is more likely that there were branches on which the main tendencies of development were realized subsequently by a number of large Mesozoic groups.

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