ISSN 0031-0301, Paleontological Journal, 2006, Vol. 40, No. 1, pp. 66–74. © Pleiades Publishing, Inc., 2006.
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# New Upper Permian Superfamily Compositelasmatoidea (Brachiopoda, Terebratulida) from the East of the Russian Platform: The Specificity of Ontogenetic Transformations

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Received June 22, 2004

**Abstract**—A previously unknown type of ontogeny is discussed that unites features of two different types of loop development: the ancient dielasmoid type, which is typical of Upper Paleozoic terebratulids, and the angustothyridid type, which is typical of the Lower Mesozoic terebratulids. A new superfamily, Compositelasmatoidea, and a new family, Compositelasmatidae, with its type genus *Compositelasma* gen. nov., are established based on their unique ontogenetic changes.

**DOI:** 10.1134/S0031030106010072

*Key words*: Upper Permian, Lower Kazanian Substage, Sok River, Russian Platform, Chuvashskii Baitugan.

## INTRODUCTION

This paper is one of the series of papers on the Late Permian (Lower Kazanian) Terebratulida from the eastern Russian Platform. Papers of Grigorjeva (1967), Smirnova (2004a, 2004b), and Smirnova *et al.* (2004) contain references on this group. The material was collected in the Samara Region, within the Sok River basin, near the village of Chuvashskii Baitugan. Earlier, on the base of Grigorjeva's (1967) paper, all terebratulids from this region were referred to the species *Beecheria netschajewi* Grigorjeva, 1967. This may be explained by the fact that these terebratulids have not been adequately studied because of their homeomorphy, which prevents taxa of different ranks from being distinguished based on the external features. Thus, serial cross sectioning through the shell followed by reconstruction of cardinalium and brachidium is the only possible way to study the inner structures. Based on this approach, the author distinguished several new taxa as follows: the family Beecheriidae, the genera *Gruntelasma*, *Grigorjevaelasma*, *Sokelasma*, and *Campbellelasma*, and seven new species (Smirnova, 2004a, 2004b; Smirnova *et al.*, 2004). The unique preservation of the vast material made it possible to study the inner structures, to reconstruct different developmental stages, and to trace the entire ontogeny of one terebratulid group in which a composite, previously unknown type of loop development was revealed and which, based on this character, is here established as a new superfamily, Compositelasmatoidea.

## MATERIAL

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

## SYSTEMATIC PALEONTOLOGY

Order Terebratulida

Superfamily Compositelasmatoidea Smirnova, superfam. nov.

Diagnosis. Shell small, smooth or with small ventral sulcus. Dental plates present. Outer hinge plates present at all developmental stages. Inner hinge plate supported by septum or free. Crural bases connected with outer hinge plate. Brachidium passing in ontogeny through complicated developmental stages involving secondary elements. Features of dielasmoid and angustothyridid ontogenetic types present simultaneously.

Composition. One family.

### Family Compositelasmatidae Smirnova, fam. nov.

Type genus. *Compositelasm*a gen. nov.

Diagnosis. As for the superfamily.

Generic composition. Type genus.

### Genus *Compositelasma* Smirnova, gen. nov.

Etymology. From the Latin *compositus* (complicated) and Greek *elasma* (plate).

Type species. *Compositelasma evolutum* sp. nov.

Diagnosis. Shell variously shaped, mainly rounded triangular. Weak sulcus running the entire length of ventral valve. Dorsal valve rooflike. Anterior commissure angular arched. Pedicle collar present. Dental plates subparallel. Outer hinge plates horizontal or slightly inclined. Inner hinge plate[1] supported by septum, euseptoid, or free. Loop branches narrow; transverse band arched. Two ventrally directed vertical plates involved in the development of brachidium. In one plate, the dielasmoid (mainly Paleozoic) type of development with pronounced mutationelliform developmental stage is observed during early ontogenetic stages and disappears in later ontogenetic stages. Modifications of the other ventrally directed plate exist during all developmental stages and correspond to the stages of the angustothyridid (Mesozoic) type of development.

Species composition. Type species.

***Compositelasma evolutum* Smirnova, sp. nov.**

Plate 8, figs. 1–4

Etymology. From the Latin *evolutus* (developed).

Holotype. PIN, no. 4898/2391; complete shell, eastern Russian Platform, Sok River, village of Chuvashskii Baitugan; Upper Permian, Lower Kazanian.

Description. The shell is small, rounded pentagonal, rarely pyriform with an elongated umbo. The valves are equiconvex, or the ventral valve is slightly more convex than the dorsal. The anterior commissure is arched and slightly angular in the middle. The lateral commissures are broadly arched. The hinge line is long and curved at a right angle. The maximum width is near the anterior margin, while the maximum convexity is in the middle. The ventral valve is narrow in the umbonal region and broadens considerably anteriorly. The sulcus is shallow, has gentle slopes, and almost reaches the umbo. The lateral surfaces of the anterior part of the valve are flattened. The umbo is high and curved. The foramen is umbonal and labiate. The pseudoarea is high, concave, and is restricted by sharp beak ridges. The apical angle is 65°–70°. The dorsal valve is rooflike with a midline elevation along its full length. The lateral margins of the valve are flattened.

Dimensions in mm and ratios:

| Specimen no. | L | W | T | W/L | T/L |
|---|---|---|---|---|---|
| Holotype 4898/2391 | 20.5 | 15.5 | 9.6 | 0.75 | 0.47 |
| 4898/2392 | 17.3 | 14.5 | 8.5 | 0.84 | 0.49 |
| 4898/2393 | 16.7 | 14.4 | 7.8 | 0.86 | 0.48 |
| 4898/2394 | 15.9 | 13.4 | 7.8 | 0.84 | 0.49 |
| 4898/2395 | 14.3 | 11.8 | 7.2 | 0.82 | 0.51 |

Shell interior (Figs. 7, 8g). The pedicle collar is angular in cross section. The dental plates are long and bound narrow delthyrial cavities. The teeth enter the dental sockets obliquely, and there are complementary denticles. The inner hinge plate is either free or is supported by a septum or euseptoid. A high, narrow crest is present in the middle concave part of the inner hinge plate and extends for a considerable distance from the umbo. The outer hinge plates are wide, horizontal, and inclined to the inner socket ridges. The crural bases are narrow, with pronounced ventral tips in adult developmental stages. The crural processes are short. The loop branches are narrow. The transverse band of the loop is strongly arched. The length of the loop is two-fifths of the length of the dorsal valve.

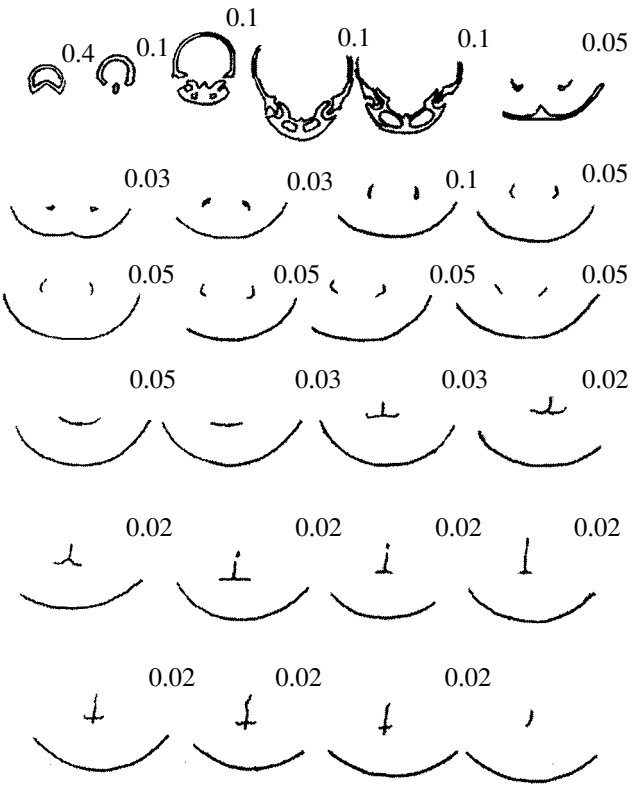



**Fig. 1.** *Compositelasma evolutum* sp. nov.; specimen PIN, no. 4898/2397, serial sections through a 2.9-mm-long shell; figures indicate distances between the sections in mm.

Ontogeny. The 2.9-mm-long shell (Figs. 1, 8a) has a curved pedicle collar. Teeth are absent. The crest in the middle of the inner hinge plate is well pronounced. The inner hinge plates are supported by the septum along the entire length. Two ventral vertical plates are almost fused together and can be distinguished only in cross sections. The first vertical plate, i.e., the plate connected with the dielasmoid type of development, is located in the posterior half of the brachidium and is supported by the joined branches of the brachidium, which have a distinct ventral bend at their junction. This stage corresponds to the early mutationelliform stage of the dielasmoid type of brachidium development. The second ventral vertical plate, i.e., the

[1] This term was proposed instead of *septal plates* in *Treatise on Invertebrate Paleontology: Part H. Brachiopoda* by Lee *et al.* (2004).

Plate 8

1a

1b

1c

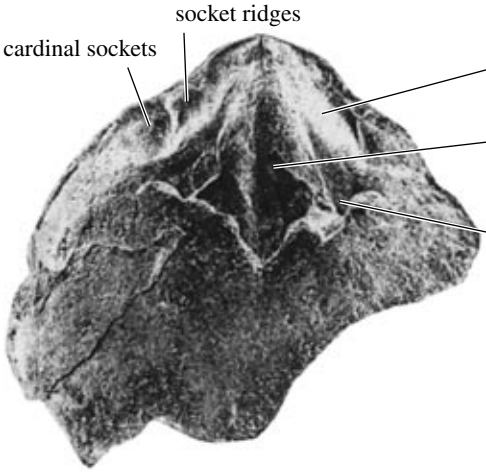
1d

2a

2b

2c

2d

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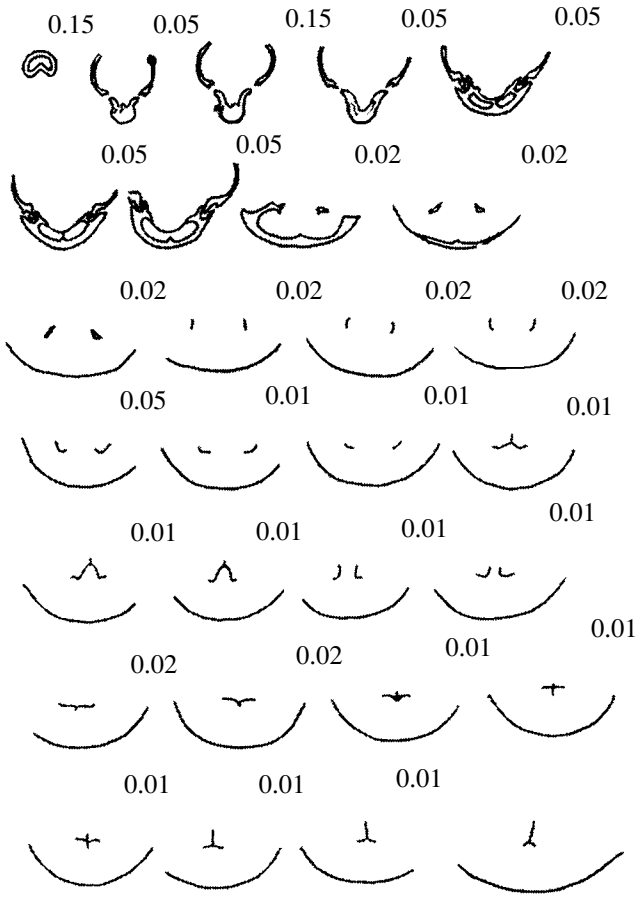


**Fig. 2.** *Compositelasma evolutum* sp. nov.; specimen PIN, no. 4898/2398, serial sections through a 3.2-mm-long shell; figures indicate distances between the sections in mm.

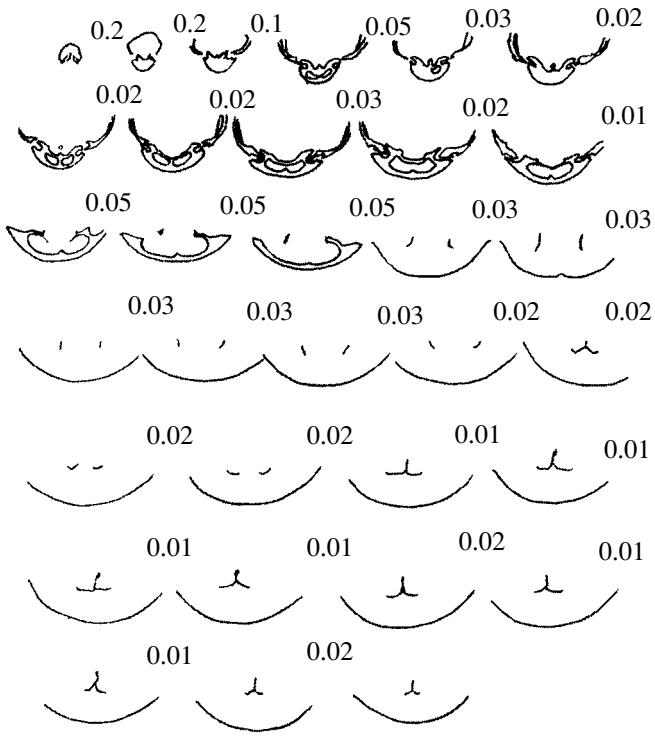


**Fig. 3.** *Compositelasma evolutum* sp. nov.; specimen PIN, no. 4898/2399, serial sections through a 4.2-mm-long shell; figures indicate distances between the sections in mm.

plate connected with the angustothyridid type of brachidium development, is located on the anterior half of the brachidium and has a short dorsal tip projecting beyond the brachidium and a small thickening on the ventral tip, i.e., features corresponding to the late centronelloid stage. This thickening gives rise to secondary elements that subsequently form the transverse band of the loop.

The 3.2-mm-long shell (Figs. 2, 8b) has a curved pedicle collar. Dental plates are absent. The inner hinge plate is supported by a low septum that is free in the anterior half. The crural bases have pronounced ventral and dorsal tips. Two ventrally directed vertical plates are distinctly differentiated and narrowly spaced. The brachidium is deeply curved ventrally, at the junction with the first ventral vertical plate, i.e., corresponding to the mutationelliform stage. The brachidium branches fuse to form a single flat surface on which the second ventral plate with a thickening on the ventral tip forms. The plate has a short dorsal tip projecting beyond the brachidium. This structure corresponds to the late centronelloid stage.

The 4.2-mm-long shell (Pl. 8, fig. 3; Figs. 3, 8c) has an angular pedicle collar. Short dental plates are placed close to the shell wall. Each tooth has two denticles. The polished cross sections clearly show a crest in the middle of the inner hinge plate. The hinge plate is free in the anterior half. The crural bases have short ventral and dorsal tips. The first ventral vertical plate is small and well differentiated and is supported by the ventrally curved domelike branches of the brachidium—an early mutationelliform stage. Anteriorly, the branches of the brachidium form a horizontal surface with a well-pronounced second ventral vertical plate that has a thickening on the ventral tip—a late centronelloid stage.

Explanation of Plate 8

**Figs. 1–4.** *Compositelasma evolutum* sp. nov.: (1) holotype PIN, no. 4898/2391, ×2: (1a) dorsal valve, (1b) ventral valve, (1c) lateral view, and (1d) anterior margin; (2) specimen PIN, no. 4898/2396, ×2: (2a) dorsal valve, (2b) ventral valve, (2c) lateral view, and (2d) anterior margin; (3) specimen PIN, no. 4898/2404, dorsal valve, detail of cardinalium, ×15; and (4) specimen PIN, no. 4898/2405, dorsal valves, detail of cardinalium, ×15; eastern Russian Platform, Samara Region, village of Chuvashskii Baitugan, Sok River basin; Upper Permian, Lower Kazanian Substage.

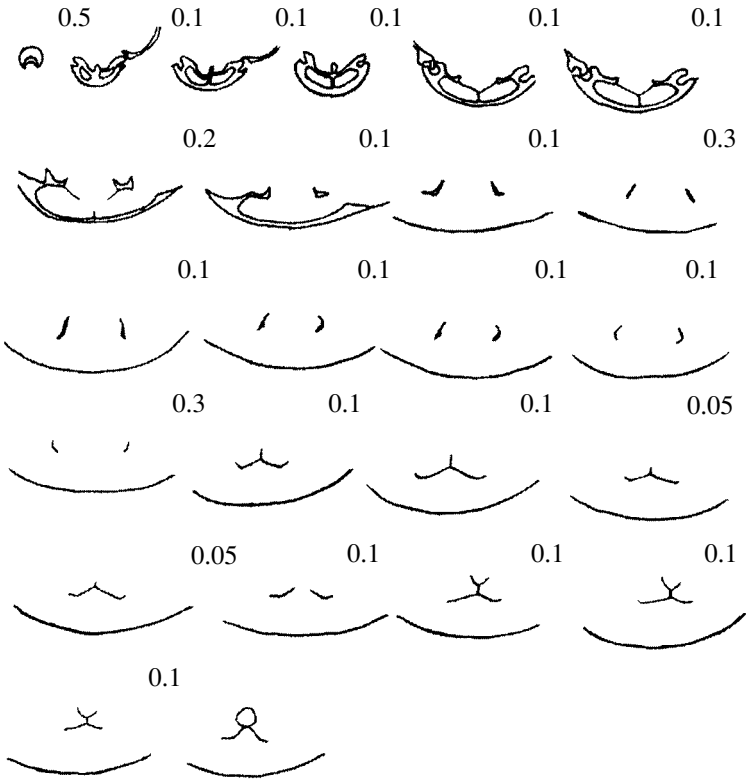


**Fig. 4.** *Compositelasma evolutum* sp. nov.; specimen PIN, no. 4898/2400, serial sections through a 5.3-mm-long shell; figures indicate distances between the sections in mm.

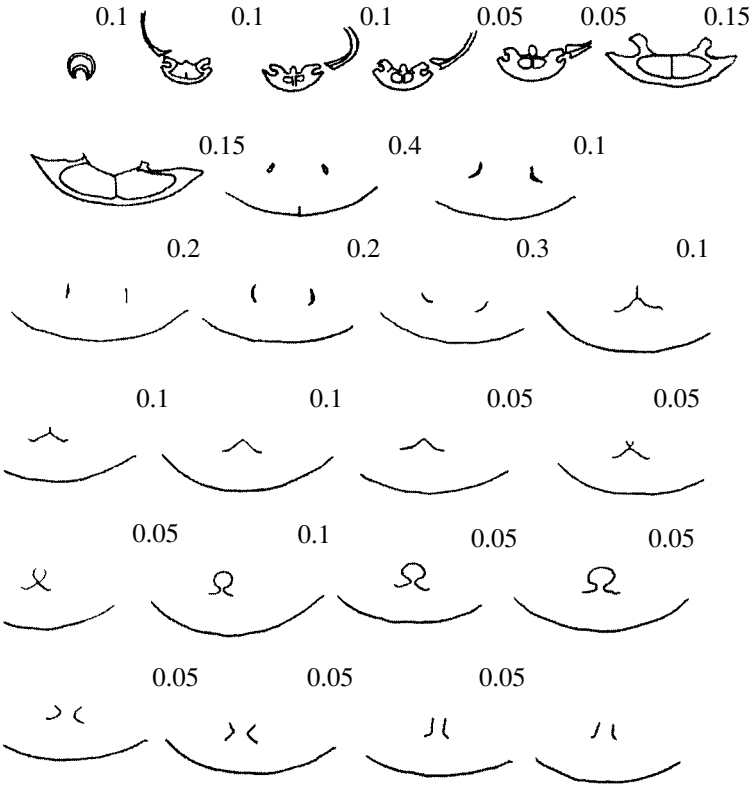


**Fig. 5.** *Compositelasma evolutum* sp. nov.; specimen PIN, no. 4898/2401, serial sections through a 6.2-mm-long shell; figures indicate distances between the sections in mm.

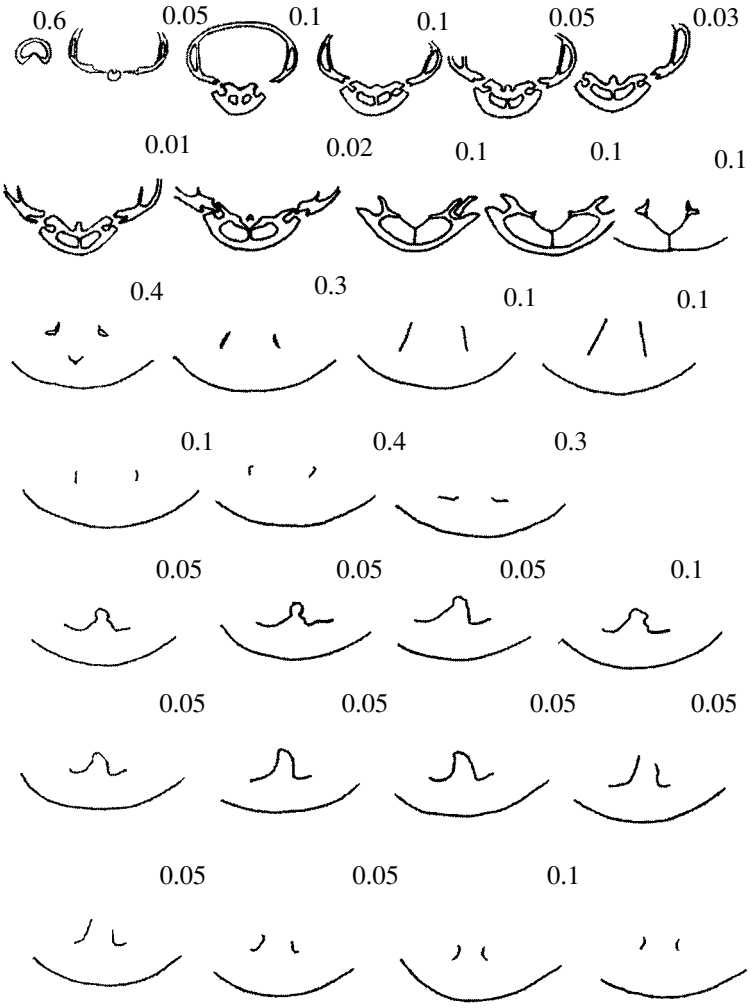


**Fig. 6.** *Compositelasma evolutum* sp. nov.; specimen PIN, no. 4898/2402, serial sections through a 7.4-mm-long shell; figures indicate distances between the sections in mm.

The 5.3–5.8 mm long shell (Pl. 8, fig. 4; Figs. 4, 8d) has a well-pronounced pedicle collar. Dental plates are absent. The crural bases are poorly developed. The inner hinge plate has a high crest in the middle and is supported by a high septum. Stages corresponding to two types of ontogenetic changes, dielasmoid and angustothyridid, are distinguished. The well-pronounced first ventral vertical plate and the ventral curvature at the junction of this plate and branches of the brachidium correspond to the mutationelliform stage of the dielasmoid type of development. The second ventral vertical plate has a split that shifts downwards along the plate to form a hood—a campagiform stage of the angustothyridid type of development. The structures corresponding to both types of development are separated by a small distance on the brachidium surface.

The 6.2-mm-long shell (Figs. 5, 8e) has an angular pedicle collar, short, weakly developed dental plates, and a well-pronounced crest on the inner hinge plate, which is supported by the septum. The first ventral vertical plate is absent. There is a small hood at the junction of the branches of the brachidium and the second ventral vertical plate. The hood migrates downwards along the vertical plate. The increased ventral curvature results in the separation of the branches of brachidium. This stage corresponds to the dictiothyridid stage of the angustothyridid type of development.

The 7.4-mm-long shell (Figs. 6, 8f) has an angular pedicle collar, distinct short dental plates, and a crest supported by a high septum on the inner hinge plate. The dorsal walls of the hood are reduced, and only remnants of their junction remain. The ventral wall of the hood makes a sharp bend, which subsequently passes into the transverse band of the loop. This stage may be compared with the late dictiothyridid stage.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage, eastern Russian Platform.

M a t e r i a l. Forty well-preserved specimens from the type locality.

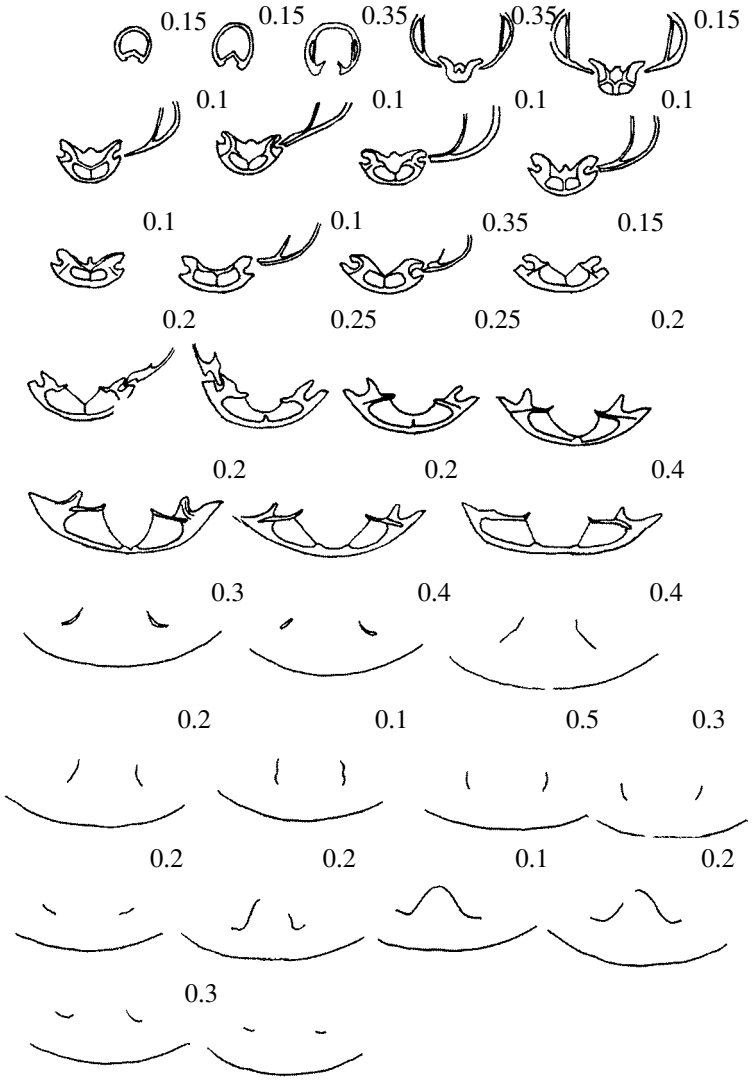


**Fig. 7.** *Compositelasma evolutum* sp. nov.; specimen PIN, no. 4898/2403, serial sections through a 14-mm-long adult shell; figures indicate distances between the sections in mm.

## CONCLUSIONS

Until recently, the complex development of the brachidium on the basis of the appearance of secondary elements was considered to be restricted to the Mesozoic and Cenozoic terebratulids. Dagis (1968, 1972) revealed the terebratuloid, loboidothyridid, angustothyridid, and zeilleroid types of ontogenetic changes in Triassic and Jurassic terebratulids and the dielasmoid type in Late Paleozoic terebratulids. All these types of the development of brachidium are characterized by the formation of the adult stages on the basis of a single vertical plate. Smirnova (2001) was the first to reveal that Late Permian terebratulids may have a brachidium with secondary elements that may cause its complicated development. Thus, the terebratuloid and loboidothyridid types of the brachidium development have come to light and made it possible to establish the appearance of the superfamilies Terebratuloidea and Loboidothyroidea in the Upper Permian of the northern Pamirs. The ontogenetic changes of the brachidium in the Late Permian terebratulids of the Russian Platform were studied for the first time. The abundance of well-preserved shells of different sizes facilitated the investigations. The method of serial cross sectioning with successive reconstruction of cardinalium and brachidium for different ontogenetic stages was used. More than 60 series of polished cross sections were made. The elements of inner structures are very well preserved even in the smallest specimens because the shell interior was filled with fine terrigenous material.

The presence of two ventrally directed vertical plates at early and middle stages of terebratulid ontogeny was discovered for the first time. The first plate is connected with the dielasmoid type of brachidium development, which is mainly characteristic of Paleozoic terebratulids. On the basis of the second plate, the

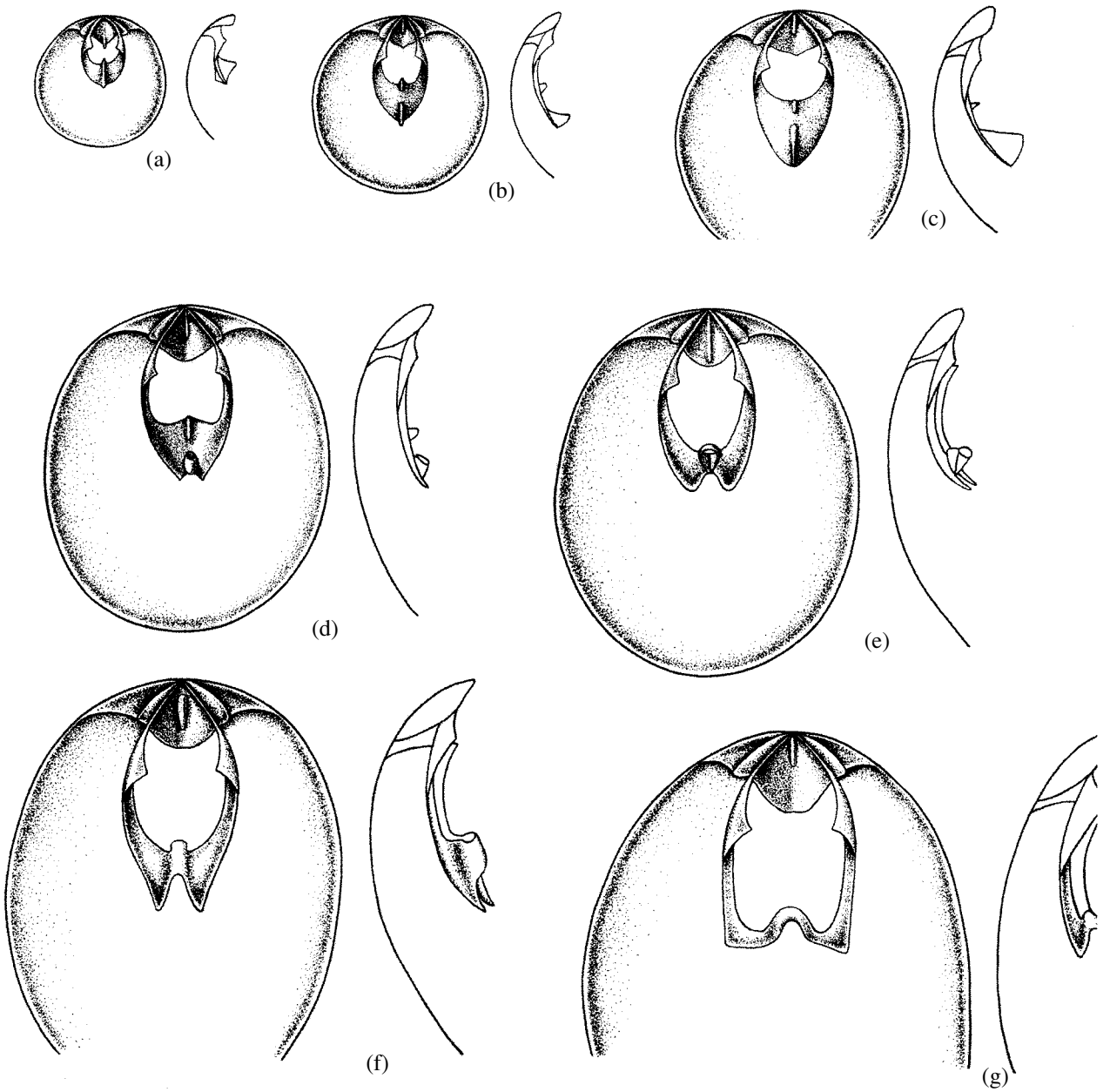


**Fig. 8.** *Compositelasma evolutum* sp. nov.; reconstruction of the inner structures in specimens with lengths (a) 2.9 mm, (b) 3.2 mm, (c) 4.2 mm, (d) 5.3 mm, (e) 6.2 mm, (f) 7.4 mm, and (g) 14 mm.

stages connected with the angustothyridid type of development, characteristic of Triassic terebratulids, are formed. Peculiar features of the revealed type of brachidium development are the simultaneous existence of two different types of development at early stages and the replacement of the dielasmoid type of development by the angustothyridid type in older forms. The sequential ontogenetic stages were traced for both types of the brachidium development. The superfamily Dielasmatoidea is widely distributed in the Permian and, thus, the dielasmoid type of the brachidium development dominates. The appearance of the mixed type of the brachidium development cannot be unambiguously explained. In my opinion, the most plausible explanation is that this type of development, which was new for the Permian, was formed from the common dielasmoid type, in order to create stronger inner structures. This type of development is unknown in more recent epochs and, thus, appears to be a dead-end branch. Studies conducted in the Late Permian basins of the Tethys (northern Pamirs) (Smirnova, 2001) and in the Boreal paleozoogeographical region

(Russian Platform) show that in these areas the complicated development and appearance of secondary elements of the loop occurred simultaneously in different terebratulid groups. We have good reason to believe that there is a certain evolutionary level on which the evolutionary potential of terebratulids was realized through the formation of a more complex brachidium at different developmental stages. It was the earliest attempt to create a new and, possibly, more perfect type of loop development. In the Mesozoic, such attempts gave rise to different types of loop development that are characteristic of some superfamilies. The triangular loop that was formed by the mixed type of development on the basis of the dorsal vertical plate is not homologous to the dielasmoid and terebratuloid loops, which were formed by the transformation of the ventral vertical plate. The triangular loop may be homologous to the loops formed by the loboidothyridid and angustothyridid types of development.

The analysis of information, which was obtained in the ontogenetic studies of the Late Permian terebratulids of the Russian Platform, revealed the specificity of evolutionary changes in the Late Paleozoic terebratulids and the origin of the complicated transformations of the brachidium in the order Terebratulida and made it possible to establish a new, mixed type of the loop development, to determine the time of the emergence of the secondary elements of the loop, which are the basis for its complicated metamorphosis, and to note the presence of Mesozoic elements in the loop development.

## ACKNOWLEDGMENTS

I am grateful to A.A. Madison and S.V. Moloshnikov, graduate students at the Department of Paleontology of Moscow State University, for material that they collected by treatment of washed clays.

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