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Mantle expansion upon the conch in the Late Devonian ammonoid *Erfoudites*

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ABSTRACT:

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Specimens of the Late Devonian ammonoid species *Erfoudites rugosus* sp. nov. from the Rhenish Massif of Germany show an additional wrinkled structure that covers the body chamber ornament. The pattern closely resembles the dorsal wrinkle layer known from many ammonoids; the course of the wrinkles is radial, partially following the growth line course. This wrinkle structure is interpreted as resulting from a secretion of the mantle, which expanded ventrally or dorsally over the conch.

Key words: Ammonoids, *Erfoudites rugosus* sp. nov., Germany, Devonian.

INTRODUCTION

After many decades of using Recent *Nautilus* as a living example for hypotheses on ammonoid soft body morphology and mode of life of ammonoids, many palaeontologists now prefer living squids as better models. This is based on the view that ammonoids may be more closely related to squids than to nautiloids (SCHINDEWOLF 1933, ERBEN 1966, BERTHOLD & ENGESER 1987), supported by claims that they share more synapomorphic characters with coleoids than with *Nautilus* (summarised by JACOBS & LANDMAN 1993). Many reconstructions of ammonoid soft bodies have been published in recent years, showing the animal with eight or ten arms, and suggesting that at least some ammonoids might have enclosed parts of their shell within their mantle (DOGUZHAEVA & MUTVEI 1989, 1991).

Up to the present, reconstructions of Palaeozoic ammonoids have only rarely been achieved, for example by x-ray examinations of crushed specimens from the Hunsrück Shale (STÜRMER 1969, ZEISS 1969). However, interpretations of the material may be equivocal. The lack of information on Palaeozoic ammonoids is particularly due to the fact that the recrystallisation of the shell wall only rarely permits the investigation of ultrastructural features. Hence identification of different shell wall elements is usually prevented.

Conchs of Late Devonian ammonoids of the goniatite genus *Erfoudites* from different localities in the Rhenish Massif in Germany (Text-fig. 1) may provide data for the reconstruction of the soft body. The ammonoids described here display a wrinkled structure on the outside of the body chamber, which partly covers the shell surface. The structure has much in common with the dorsal wrinkle layer, occurring mostly on the inside of the conch and is reported from many Devonian ammonoids (CLAUSEN 1969, WALLISER 1970, HOUSE 1971, DOGUZHAEVA 1981, KORN 1985). An expansion of the mantle over the conch is suggested.

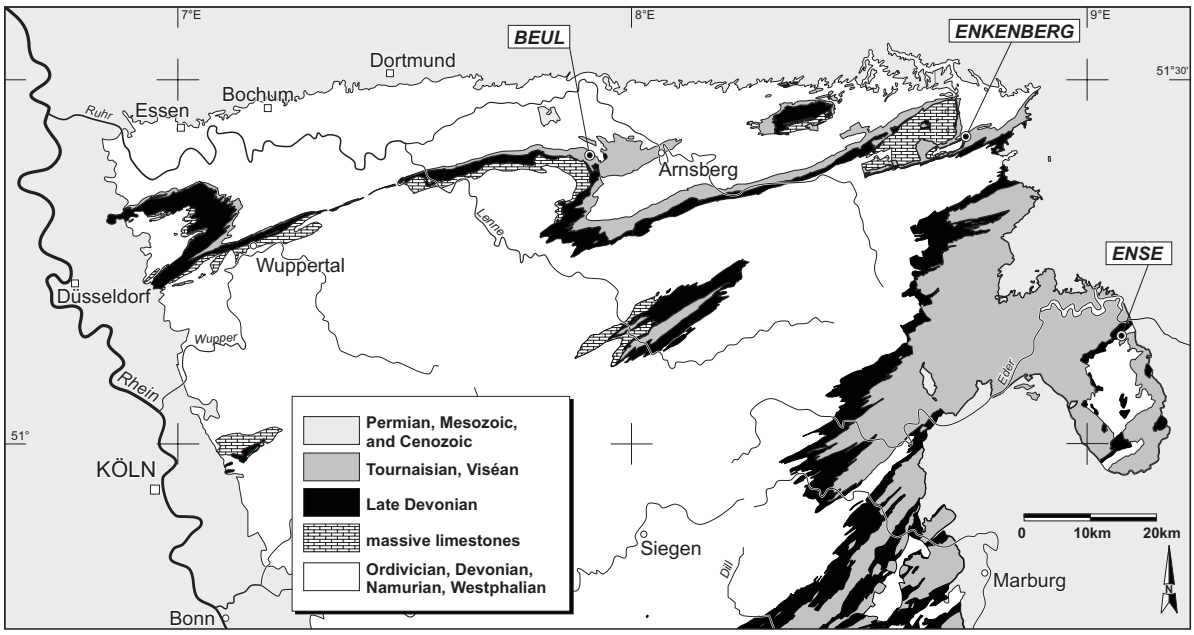

Fig. 1. Map showing localities of Late Devonian rocks which yielded specimens of *Erfoudites rugosus* sp. nov.

SYSTEMATIC ACCOUNT

Suborder Tornoceratina WEDEKIND 1918
Family Sporadoceratidae MILLER & FURNISH 1957
Genus *Erfoudites* KORN 1999

TYPE SPECIES: *Erfoudites zizensis* KORN 1999.

GENERIC COMPOSITION:
zizensis: *Erfoudites zizensis* KORN 1999. *Platyclymenia annulata* Zone, eastern Anti-Atlas, Morocco.
rherisensis: *Erfoudites rherisensis* KORN 1999. *Protoxyclymenia dunkeri* Zone, eastern Anti-Atlas, Morocco.
rotundolobatus: *Sporadoceras rotundolobatum* SCHINDEWOLF 1924. probably *Protoxyclymenia dunkeri* Zone, Thuringia, Germany.
spirale: *Sporadoceras spirale* WEDEKIND 1918. Lower *Clymenia* Stufe, Rhenish Massif, Germany.
ungeri: *Goniatites ungeri* MÜNSTER 1840. Uebergangskalk, Franconia, Germany.
rugosus: *Erfoudites rugosus* sp. nov. *Platyclymenia annulata* Zone, Rhenish Massif, Germany.

GENUS DEFINITION: Genus of Sporadoceratidae with conch discoidal to thickly discoidal, involute in all stages; ornament of slightly biconvex growth lines and fine spiral lines; suture line with deep, broadly rounded A1 lobe, small, rounded A2 lobe and small, V-shaped E lobe.

COMPARISONS: The conch form and suture line of *Erfoudites* are similar to those of *Maeneceras*, but the new genus is easily discriminated from other genera of Sporadoceratidae by the spiral ornament, and the biconvex course of its growth lines. *Erfoudites* species superficially resemble species of *Posttornoceras*, but differ in their conch parameters. The latter genus has a very high whorl expansion rate, the whorl height exceeding 65% of the diameter. In *Erfoudites* it does not reach 60%, falling inside the field of variation of typical sporadoceratids. In contrast to *Erfoudites*, *Posttornoceras* does not display spiral ornament (KORN 1999).

OCCURRENCE: The *Platyclymenia annulata* Zone, as well as the *Protoxyclymenia dunkeri* Zone (and probably ranging into the *Clymenia laevigata* Zone) of the Tafilalt of Morocco and of the Rhenish Massif, Germany.

Erfoudites rugosus sp. nov.
Text-figs 2A-J, 3A, B, 4

DERIVATION OF NAME: From Lat. *rugosus* = wrinkled, after the surface texture of the additional shell structure.

MATERIAL: Seven specimens are available for study. The holotype (SMF 60184, coll. KORN 1980) is the largest and best preserved individual, it derives from the summit of Beul near Eisborn at the northern margin of the Rhenish Massif. From the same locality, one smaller additional fragment (paratype SMF 60185, coll. KORN 1992) that displays the suture line was also collected. Four specimens (SMF 60186 to 60189) between 10 and 40 mm conch diameter come from a trench dug on Ense near Bad Wildungen in the Kellerwald. These specimens are distorted tectonically but display the well preserved conch ornament. One single specimen (SMF 60190) was surface collected on the Enken-Berg near Brilon. All the specimens are from the *Platyclymenia annulata* Zone (Late *trachytera* Zone of the conodont zonation).

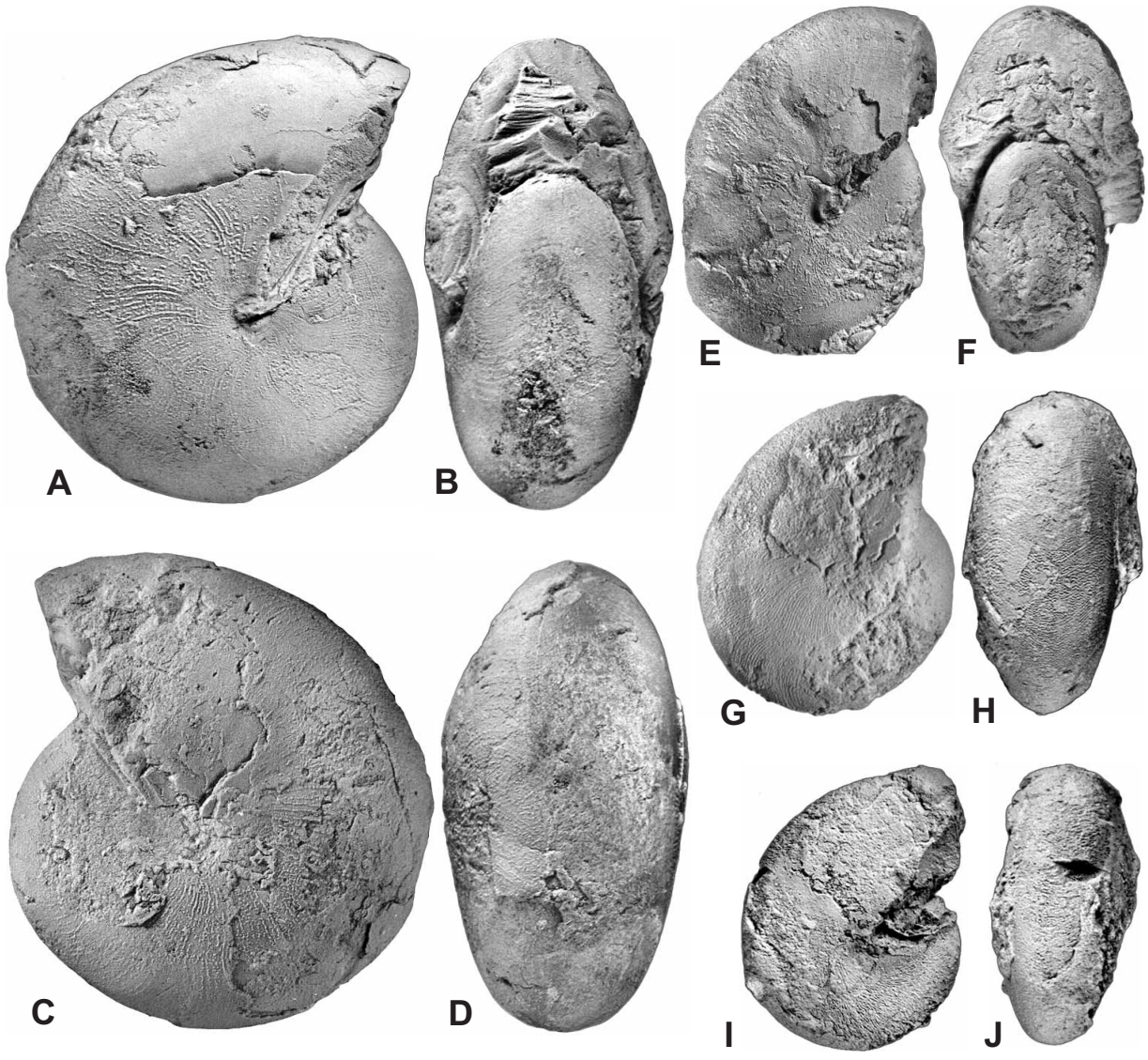

Fig. 2. *Erfoudites rugosus* sp. nov.
A-D – holotype, SMF 60184; *Platyclymenia annulata* Zone, Beul; × 1.25; E-F – paratype, SMF 60186; *Platyclymenia annulata* Zone, Ense; × 1.25; G-H – paratype, SMF 60187; *Platyclymenia annulata* Zone, Ense; × 1.75; I-J – paratype, SMF 60190; probably *Platyclymenia annulata* Zone, Enkenberg; × 1.75

Dimensions in mm:

	dm	ww	wh	uw	ah	WER	ww/dm	ww/wh
holotype SMF 60184	56.5	29.5	31.4	0	15.6	1.91	0.52	0.94
paratype SMF 60186	40.5	22	22.5	0			0.54	0.98
paratype SMF 60187	24.7	14.8	15.6	0			0.60	0.95

DIAGNOSIS: Species of the genus *Erfoudites* with thickly discoidal conch (ww/dm = 0.55) and with closed umbilicus. Ornament with fine, intensively crenulated growth lines and very fine spiral lines, together forming a reticulate pattern. The number of spirals exceeds 250, they are distributed over the entire conch.

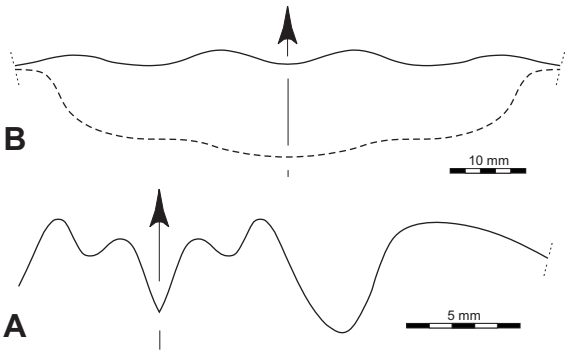

Fig. 3. Suture line, wrinkle course, and growth line course in Late Devonian *Erfoudites rugosus* sp. nov.
A. Suture line of the paratype SMF 60185; *Platyclymenia annulata* Zone, Beul; x 3; at ww = 14.3 mm, wh ca. 16.5 mm
B. Course of the wrinkles (dashed, below) and growth lines (above) of the holotype SMF 60184; *Platyclymenia annulata* Zone, Beul; x 1; at dm = 48 mm, ww = 27.7 mm, wh 29.5 mm

DESCRIPTION: The holotype is a rather well preserved specimen of 56 mm diameter that displays characters allowing an interpretation of the living animal (Text-fig. 5). The conch is thickly discoidal (ww/dm = 0.53) and is broadest at the completely closed umbilicus. Almost the entire specimen is preserved with shell, it is corroded only in a few small areas. A large fragment of the shell wall was mechanically removed, revealing the surface of the internal mould. This area belongs to the body chamber; remains of the last septum are visible in exactly half a whorl distance of the largest diameter. Both the shell ornament, and an additional wrinkled structure covering the ornament are clearly visible on this specimen.

The ornament consists of very delicate, intensively crenulated growth lines spaced at 0.1 mm. Their course is prorsiradiate and biconvex, forming a shallow dorsolateral salient, a pronounced ventrolateral salient and a deep ventral sinus (Text-fig. 3B). Fine spiral lines with spaces of 0.2 mm cross the growth lines; these number more than 250, counted from umbilicus to umbilicus. Growth lines and spiral lines appear to have the same strength and generate a beautiful reticulate pattern

An additional, irregularly distributed structure covers the shell ornament (Text-fig. 4). It consists of prominent wrinkles, which are much more conspicuous than the growth lines. This additional pattern consists predominantly of radial wrinkles, spirally arranged wrinkles, and spotlike elements. The spacing between the radial wrinkles, which have a width of 0.5 to 1.0 mm, allows recognition of the underlying shell surface with growth-lines and spiral ornament. In their course, the wrinkles largely follow the growth lines. They also form a shallow dorsolateral projection, but in the midflank area they turn back to form a shallow ventrolateral projection and a deep ventral sinus. In contrast to the prorsiradiate growth lines, they run in rursiradiate direction (Text-fig. 3B).

The internal mould is smooth except for slight undulations parallel with the growth lines. One prominent constriction formed by an internal shell thickening is visible ventrally, its course also follows that of the growth lines.

The holotype does not display the suture line; short remains of the probably last septum are visible exactly opposite the preserved aperture. The body chamber is filled with sediment, whereas the phragmocone is filled with sparry calcite.

The larger Ense specimen (SMF 60186) is an incomplete and slightly distorted conch of 36 mm in diameter, mostly preserved with shell wall. The ornament resembles that of the Beul specimen, and the additional wrinkle structure is similar, butt lacking in the last preserved 60°. The wrinkles are less prominent and regular than in the Beul specimen, they are strongest near the umbilicus where they are more spirally arranged.

The suture line (Text-fig. 3A) can be studied in a second specimen (SMF 60185) from Beul. It is typical for the genus *Erfoudites* in displaying a V-shaped and rounded first adventive lobe, a much smaller secondary adventive lobe, and a V-shaped external lobe.

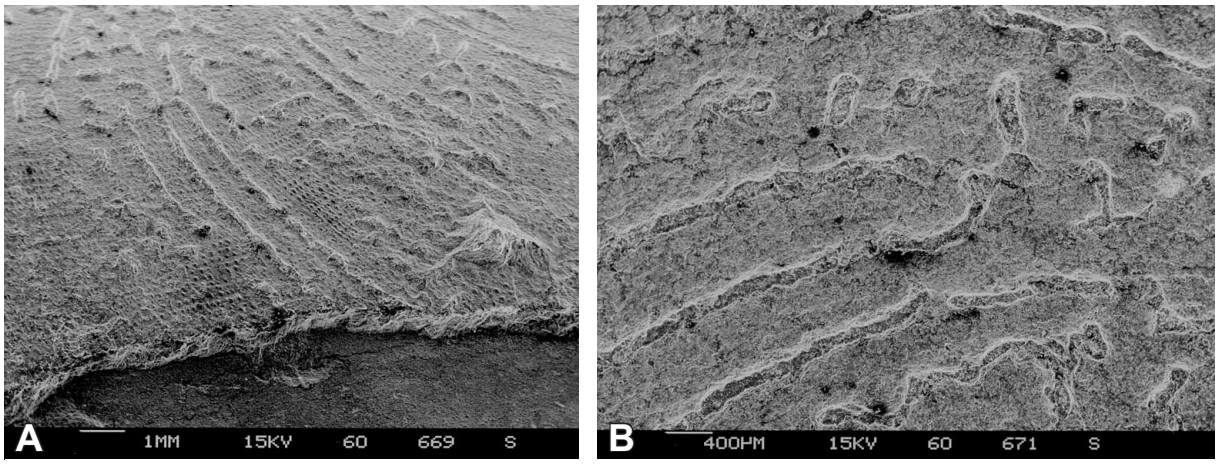

Fig. 4. SEM images of *Erfoudites rugosus* sp. nov., holotype SMF 60184; *Platyclymenia annulata* Zone, Beul

COMPARISONS: *Erfoudites rugosus* can be distinguished by the higher number of spiral lines (250) from *Erf. zizensis* KORN 1999 and *Erf. spirale* WEDEKIND 1918 (both with 150 spiral lines). *Erf. rherisensis* KORN 1999 has the same number of spirals as *Erf. rugosus*, but in that species the spirals are irregularly spaced, dissimilar to the regular spacing in *Erf. rugosus*. Furthermore, this species shows numerous steinkern constrictions on the venter, in contrast to *Erf. rugosus*, where only few constrictions occur.

STRATIGRAPHICAL AND GEOGRAPHICAL DISTRIBUTION: All the in situ collected specimens come from the *Platyclymenia annulata* Zone; the species is known from the northern and eastern margin of the Rhenish Massif.

INTERPRETATION OF THE WRINKLED STRUCTURE IN *ERFOUDITES*

Before exploring an explanation for the wrinkled structures, possible alternative origins of this structure should be discussed:

— A pathological origin can be ruled out because the structure is similarly preserved in all the available specimens of *Erfoudites rugosus*. Additionally, the regular course of the wrinkles argues against pathology.

— An origin from a parasite in the generative zone of the periostracum is also unlikely because the wrinkle pattern is not parallel to the apertural margin.

— A post-mortem taphonomic origin is not likely, because in all the specimens the structure is developed symmetrically on both sides of each conch.

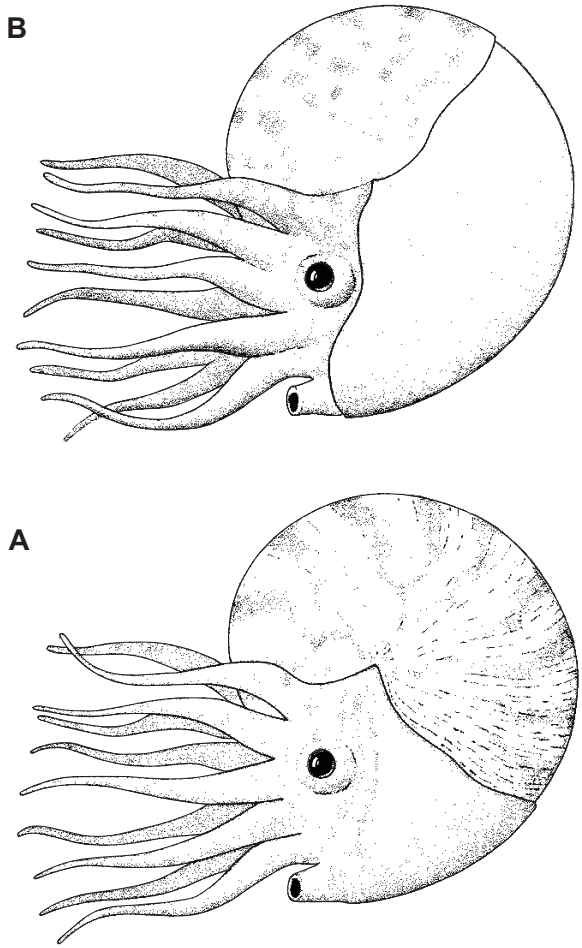

Fig. 5. Reconstruction of the shell and cephalic region of the body in *Erfoudites rugosus* sp. nov. (orientation according to the calculations for similar ammonoid conchs by TRUEMAN 1941); A. based on the assumption that a ventral mantle expansion covers 60° of the conch; B. based on the assumption that a dorsal mantle expansion covers 180° of the conch

There occurs close morphological resemblance of the structure described here with the often figured dorsal wrinkle layer of many different ammonoids. Especially the fingerprint pattern is very similar in both cases, with the combination of transverse longitudinal and dot-like structures, which only incompletely cover the shell ornament that remains visible between the wrinkles. This leads to the assumption that both structures have been secreted by the mantle. However, the origin of the wrinkle layer of Palaeozoic ammonoids is not fully understood. Mesozoic examples, however, indicate that the wrinkle layer is an additional shell layer secreted at the anterior margin of the mantle (DOGUZHAEVA 1981).

The wrinkle pattern is here interpreted as a secretion of the mantle that to some degree expanded on to the conch. It can not be stated here with certainty whether the mantle expansion developed from the ventral side in a backward direction (Text-fig. 5A), or from the dorsal side in a forward direction (Text-fig. 5B). The fact that the wrinkled pattern runs largely parallel to the apertural margin (Text-fig. 3B) may be regarded as support for a ventrally directed expansion. A dorsally proceeding expansion may also be possible because a slight mantle expansion, resulting in a dorsal wrinkle layer outside of the body chamber is known from different Palaeozoic ammonoids (HOUSE 1971, KORN 1985). Thus, a dorsal mantle expansion in *Erfoudites* may only be more fully developed.

The length of the area covered with the additional wrinkle structure cannot be stated precisely. The holotype is completely covered by the additional structure, but only 180° of its body chamber is preserved [As in all ammonoid specimens from the type horizon of the type locality at Beul, the body chamber is filled with micritic sediment, and the phragmocone is cemented by sparry calcite.] The entire body chamber probably had a length of 350-360° (data collected from *Erfoudites rherisensis* with very similar conch geometry), which means that the mantle-covered segment would have a length of approximately 180° when a dorsally proceeding mantle expansion is proposed. In the case of a ventrally proceeding expansion, the entire body chamber would bear the wrinkled layer.

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