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Morphology of the Early Whorls of Goniatites from the Carboniferous Buckhorn Asphalt (Oklahoma) with Aragonitic Preservation

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3 Text-Figures and 7 Plates

USA
Carboniferous
Goniatites
Morphology

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Morphologie und Mikrostruktur der Anfangswindungen von Goniatiten in aragonitischer Erhaltung aus dem Buckhorn-Asphalt (Oberkarbon; Oklahoma, USA)

Zusammenfassung

Die untersuchten Stücke gehören wahrscheinlich alle derselben Art oder einigen wenigen nahe verwandten Arten an. Der Durchmesser der Ammonitella beträgt etwa 0,8 mm, der Winkel der Ammonitella etwa 360°. Die ellipsoidische Anfangskammer ist von der ersten Windung der Ammonitella umgeben. Die äußere Oberfläche ist glatt ohne die geringsten Spuren von Skulptur oder Zuwachsstreifen. Im Gegensatz dazu sind Zuwachsstreifen und Liration sehr wohl auf der postembryonalen Schale vorhanden. Das dorsale Ende der Anfangskammer endet in einem dicken Flansch. Oberhalb des Flanschs befindet sich eine längliche Muskelansatzstelle an der Oberfläche der Innenseite der Anfangskammer. Die Wand der Anfangskammer besteht aus drei Lagen, deren äußerste zugleich die Dorsalwand des nächsten Umgangs ist. Die Wand des ersten Umgangs der Ammonitella besteht aus vier Schichten:
1) Innere Prismenschicht (= Muralanteil des Proseptums und der folgenden Septen).
2) Mittlere körnig/subprismatische Schicht (= eigentliche Wand der Ammonitella).
3) Sehr dünne äußere Prismenschicht.
4) Dorsalwand der nächsten (postembryonalen) Windung.

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Die Runzelschicht beginnt an der Ventralwand der Anfangskammer nahe der Ammonitellenkante. Diese Schicht ist der äußere Anteil der Dorsalwand und verschwindet bei der postembryonalen Schale. Proseptum und zweites Septum liegen im Medianschnitt auf der dorsalen Seite dicht beisammen. Das Proseptum ist prismatisch, das zweite Septum besteht aus Perlmutter. Es gibt bei den Ammonitellen dieser Goniatiten und mesozoischen Ammoniten, einschließlich der vergleichbaren Embryonalentwicklung, viele Ähnlichkeiten.

Allerdings gibt es auch einige wichtige Unterschiede betreffend die Gestalt der Ammonitella und ihre Skulptur. Die Variation der Morphologie der Ammonitella kann zur phylogenetischen Untersuchung herangezogen werden.

Abstract

We investigated the morphology and microstructure of the early whorls of goniatites with aragonitic preservation from the Upper Carboniferous Buckhorn Asphalt (Oklahoma, USA). These specimens probably all belong to the same species or to several closely related species. The ammonitella diameter is approximately 0.8 mm and the ammonitella angle is approximately 360°. The initial chamber is ellipsoidal and is surrounded by the first whorl of the ammonitella. The outer surface of the ammonitella is smooth without any trace of ornamentation or growth lines. In contrast, growth lines and lirae are present on the postembryonic shell. The dorsal end of the initial chamber terminates in a thick flange. There is an elongate muscle scar on the inside surface of the initial chamber above the flange. The wall of the initial chamber consists of three layers, the outermost of which is the dorsal wall of the next whorl. The wall of the first whorl of the ammonitella consists of four layers:

1) Inner prismatic layer (= the mural part of the proseptum and subsequent septa).
2) Middle granular/subprismatic layer (= the wall proper of the ammonitella).
3) Very thin outer prismatic layer.
4) Dorsal wall of the next (postembryonic) whorl.

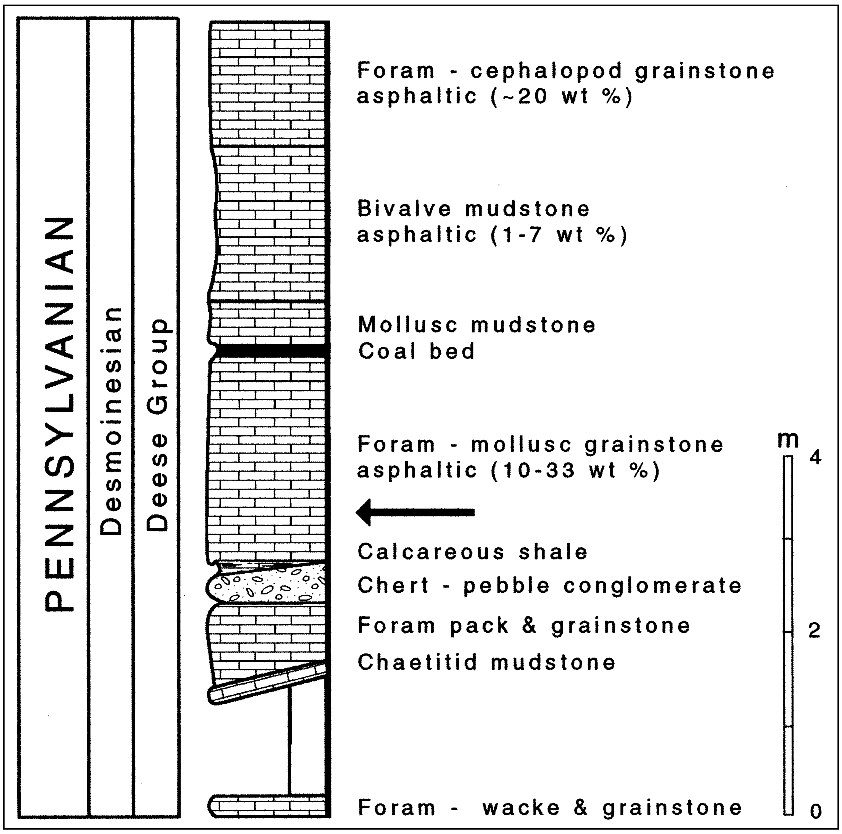
The wrinkle layer first appears on the ventral surface of the initial chamber near the ammonitella edge. This layer is the outer component of the dorsal wall and disappears on the postembryonic shell. In median cross-section the proseptum and second septum are closely spaced on the dorsal side. The proseptum is prismatic and the second septum is nacreous. There are many similarities between the ammonitellas of these goniatites and those of Mesozoic ammonoids, implying a similar mode of embryonic development. However, there are also several important differences relating to the shape of the ammonitella and its ornamentation. This variation in the morphology of the ammonitella can be used for phylogenetic analysis.

1. Introduction

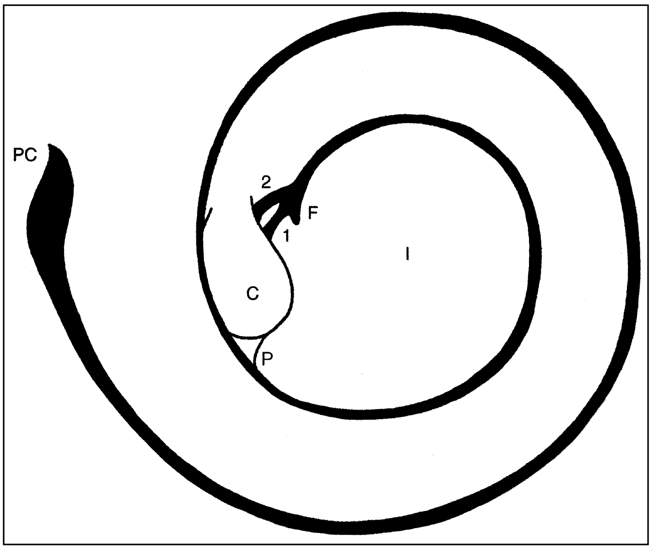
Study of the morphology of the embryonic shells of ammonoids is important both to understand the ontogenetic development of these animals as well as to document features that can be used for phylogenetic analysis. The embryonic shells of Mesozoic ammonoids have been extensively studied (see the review by LANDMAN et al., 1996). Recent studies on the embryonic shells of Paleozoic ammonoids have also added to our knowledge of these forms (TANABE et al., 1993, 1994; LANDMAN et al., 1999; KLOFAK et al., 1999). However, information about the microstructure of the embryonic shells of Paleozoic ammonoids is scant due to the fact that these ammonoids are usually poorly preserved. We report here investigations on the embryonic shells of goniatites from the Upper Carboniferous Buckhorn Asphalt of Oklahoma, USA. These specimens represent the oldest known ammonoids with aragonitic preservation. The beautifully preserved nautiloids from this locality have already been studied by GRÉGOIRE & TEICHERT (1965), RISTEDT (1971), MUTVEI (1972), CRICK & OTTENSMAN (1983), and BRAND (1987).

2. Material and Methods

The goniatites are from the Buckhorn Asphalt quarry near Ardmore, southern Oklahoma. The strata are Upper Carboniferous in age (Desmoinesian = Westphalian C) (CRICK & OTTENSMAN, 1983). The specimens occur in an asphalt rich bed within an asphaltic lens of the Boggy Formation, which is part of the Deese Group (Text-Fig. 1; CRICK & OTTENSMAN, 1983; BRAND, 1987). These beds are informally referred to as the Buckhorn Asphalt. The sediments are composed of a bioclastic carbonate rich in



Text-Fig. 1.
Stratigraphic section of the Buckhorn Asphalt quarry, southern Oklahoma, USA.
The goniatites are from the interval marked by the arrow.
Modified from BRAND (1987).



Text-Fig. 2.
Median cross-section through the embryonic shell of a goniatite.
I = initial chamber; F = flange; 1 = proseptum or first septum; 2 = second septum; C = caecum; P = prosiphon; PC = primary constriction.

molluscan debris. The asphalt resulted from the migration of hydrocarbon fluids after the deposition of the molluscs (CRICK & OTTENSMAN, 1983). Because of the asphalt, the original aragonite of the specimens is preserved.

There are about a dozen specimens, six of which are described in this study. They are reposited in the American Museum of Natural History (AMNH). Most of the specimens are hollow and are the nuclei of larger juveniles or adults. The ammonoid fauna of the Buckhorn Asphalt mainly consists of goniatites (9 species) and one species of prolecanitid (BEGHTEL, 1962; UNKLESBAY, 1962). On the basis of this faunal list and comparisons with known material, our specimens are identified as goniatites. However, a species-level identification is not possible.

The specimens were viewed under scanning electron microscopy (SEM). Three specimens were embedded in epoxy and serial sections were prepared parallel to the median plane. X-ray diffraction analysis was performed on a specimen of an orthoconic nautiloid from the same beds. It was composed of 70 % aragonite and 30 % calcite. The calcite forms a cement covering the surfaces of the shell and septa and consists of two phases differing in magnesium content.

3. Terminology

The terms used to describe the embryonic shells of goniatites are illustrated in Text-Fig. 2 and are defined in LANDMAN et al. (1999) and LANDMAN & WAAGE (1982). The embryonic shell (= ammonitella) consists of an ellipsoidal initial chamber followed by approximately one planispiral whorl. This whorl terminates in the primary constriction and accompanying varix, which is a thickening of the outer shell wall. The dorsal end of the initial chamber terminates in the flange. The first septum (proseptum) differs in shape from all subsequent septa. The siphuncle originates in the initial chamber as a swelling, known as the caecum. It is attached to the inside surface of the initial chamber by means of the prosiphon. The ammonitella diameter, ammonitella angle, and initial chamber diameter are defined in LANDMAN et al. (1996, Fig. 3).

4. Ammonitella

4.1. Size and Shape

The size and shape of the ammonitella is similar among specimens, suggesting that all specimens belong to the same species or to closely related species (Pl. 1, Fig. 1; Pl. 2, Fig. 1; Pl. 3, Fig. 1). The ammonitella is difficult to measure in most specimens because it is not completely free from the rest of the shell. The most accurate measurements are in median cross-section. In AMNH 46551 the ammonitella diameter is 770 µm, the ammonitella angle is 359°, and the initial chamber diameter is 440 µm. These measurements are comparable to those in other goniatites (TANABE et al., 1994; LANDMAN et al., 1996).

The initial chamber is circular in median cross-section and elliptical in transverse cross-section and is surrounded by the first whorl of the ammonitella (Pl. 2, Fig. 2). The umbilical portion of the initial chamber is not exposed.

4.2. Outer Surface

The outer surface of the ammonitella does not show any trace of ornamentation (Pl. 1, Figs. 1, 5; Pl. 2, Fig. 1; Pl. 3, Fig. 1). It is perfectly smooth without any tubercles, growth lines, or lirae. Ornamentation first appears immediately adoral of the ammonitella edge (Pl. 1, Fig. 1).

4.3. Initial Chamber

The dorsal end of the initial chamber terminates in the flange (Text-Fig. 3A; Pl. 2, Figs. 2, 5, 6; Pl. 3, Fig. 2). In median cross-section the flange is nearly twice as thick as the adjacent wall. In AMNH 46550 the thickness of the flange is 4.6 µm whereas the thickness of the adjacent wall is 2.6 µm.

AMNH 46552 is hollow and provides a view of the interior of the initial chamber (Pl. 2, Fig. 2). The edge of the flange is uneven with a rounded tip. The flange extends back onto the inside surface of the initial chamber and ends in an irregular margin (Pl. 2, Fig. 6).

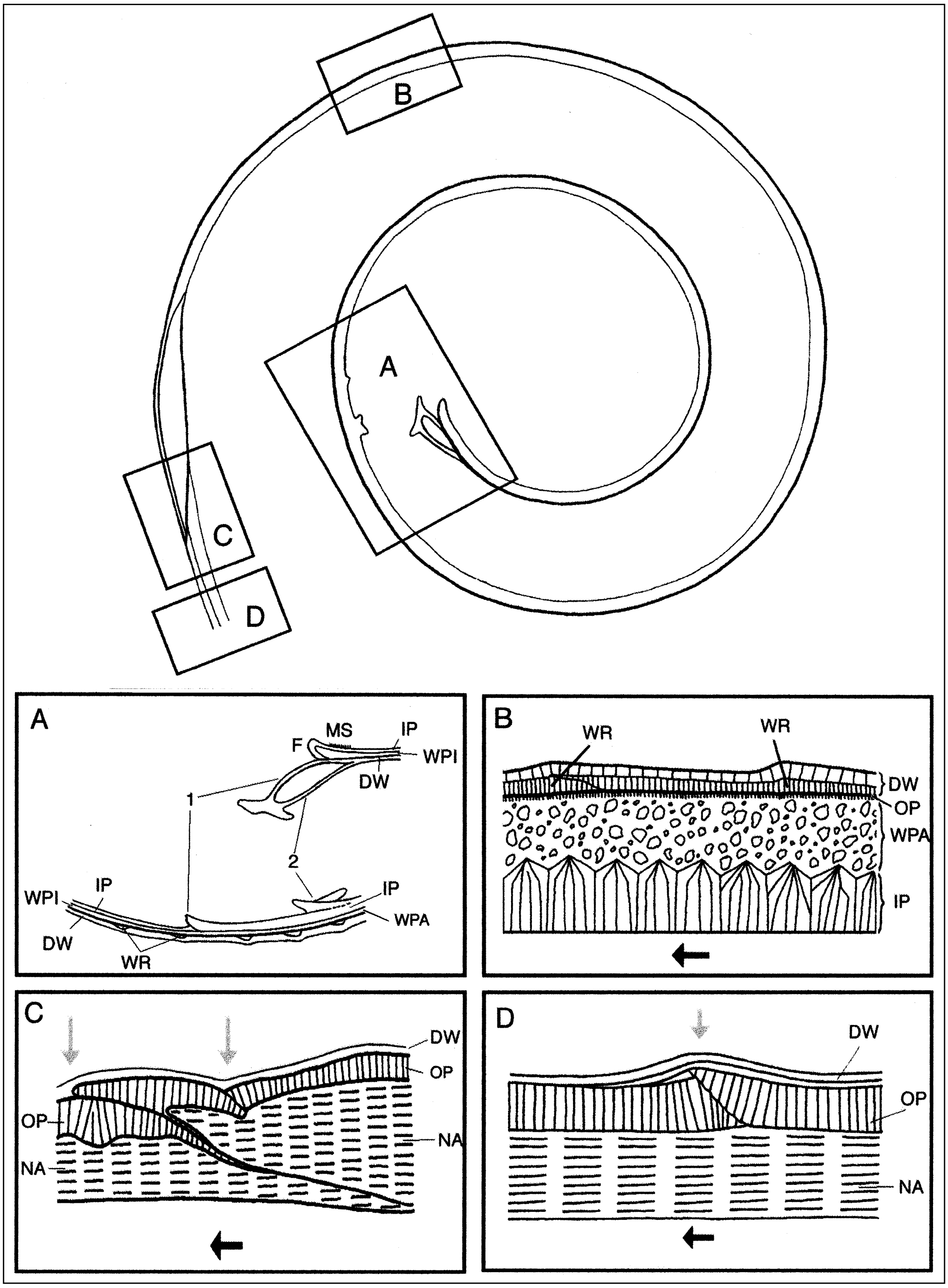
There is a broad band with tuberculate texture immediately above the flange (Pl. 2, Figs. 2, 5, 6). It is 15–25 µm wide and parallels the flange along its entire length. A similar band has been reported in other goniatites and has been interpreted as a muscle scar that formed inside the initial chamber (LANDMAN et al., 1999, Fig. 3F).

The wall of the initial chamber on the ventral side of the proseptum is 3.5 µm thick in median cross-section in AMNH 46550. It consists of three layers (Text-Fig. 3A; Pl. 2, Fig. 4). The innermost layer represents the mural part of the proseptum. The middle layer is the main component of the wall of the initial chamber (= “the wall proper of the initial chamber” [KULICKI, 1996]). The outermost layer is the dorsal wall of the next whorl, which shows wrinkles.

4.4. First Whorl

The wall of the first whorl is 7 µm thick midway between the first two septa in median cross-section in AMNH 46550. The wall thickness abruptly increases adoral of the second septum where the wall is approximately 10 µm thick (Pl. 4, Figs. 1, 2). This increase in thickness is due to an increase in the thickness of the innermost layer, i.e., the mural part of the septa.

The microstructure of the wall of the first whorl is visible in median cross-section in AMNH 46550 (Text-Fig. 3B; Pl. 4, Figs. 1–4; Pl. 5, Figs. 1, 2; measurements of the



Text-Fig. 3.
Median cross-section through the embryonic shell of a goniatite.
The letters indicate the locations of the close-ups shown below.

A) Close-up of the initial chamber in the vicinity of the first two septa.
DW = dorsal wall; F = flange; IP = inner prismatic layer; MS = muscle scar; WPA = wall proper of the ammonitella; WPI = wall proper of the initial chamber; WR = wrinkle layer; 1 = first septum (proseptum); 2 = second septum.
B) Close-up of the wall of the first whorl.
The arrow indicates the adoral direction. DW = dorsal wall; IP = inner prismatic layer; OP = outer prismatic layer; WPA = wall proper of the ammonitella; WR = wrinkle layer.
C) Close-up at the ammonitella edge.
The left vertical arrow indicates the ammonitella edge; the right vertical arrow, a break in the shell adapical of the ammonitella edge. The horizontal arrow indicates the adoral direction. DW = dorsal wall; NA = nacreous layer; OP = outer prismatic layer.
D) Close-up of the wall of the postembryonic shell showing a lira in the outer prismatic layer (vertical arrow).
The horizontal arrow indicates the adoral direction.
DW = dorsal wall; NA = nacreous layer; OP = outer prismatic layer.

thickness are based on Pl. 4, Fig. 4). The wall consists of four layers. The inner prismatic layer represents a continuation of the mural part of the septa and is 5 µm thick. The middle layer is granular/subprismatic and represents the main component of the wall of the first whorl (= “the wall proper of the ammonitella” [KULICKI, 1996]). It is approximately 6 µm thick. The outer prismatic layer is very thin, 0.5 µm thick. The surface of this layer is flat because no ornamentation is present. This layer forms a sharp boundary with the dorsal wall of the next whorl, which shows wrinkles. The dorsal wall has a maximum thickness of approximately 2 µm (15 % of the thickness of the ventral wall).

4.5. Aperture

The ammonitella terminates in the primary constriction and accompanying varix (Pl. 1, Figs. 1–4; Pl. 2, Fig. 1). The ammonitella edge is straight without any sinus. The shell wall appears to be bunched up or pleated near the ammonitella edge along the umbilical seam (Pl. 1, Figs. 4, 5).

The ammonitella edge is visible in median cross-section (Text-Fig. 3C; Pl. 5, Fig. 5). The outer prismatic layer of the ammonitella thins in an adoral direction and the primary varix appears. In several specimens there is a break in the outer prismatic layer immediately adapical of the ammonitella edge (Text-Fig. 3C; Pl. 5, Fig. 5).

4.6. Proseptum and Second Septum

In median cross-section the first two septa are closely spaced on the dorsal side (Text-Fig. 3A; Pl. 3, Fig. 2). The proseptum is approximately 3 µm thick and is composed of prismatic crystals oriented perpendicular to the surface of the septum (Pl. 3, Fig. 3). On the ventral side, the proseptum represents a continuation of the inner prismatic layer of the initial chamber and first whorl (Text-Fig. 3A; Pl. 4, Figs. 1, 2). On the dorsal side, it represents a continuation of the dorsal wall of the first whorl (Text-Fig. 3A).

The second septum is 2.5 µm thick in median cross-section. It is composed of nacreous lamellae oriented parallel to the surface of the septum (Pl. 3, Fig. 4). The second septum shows the same relationship with the outer wall as do all subsequent septa.

5. Postembryonic Shell

5.1. Outer Surface

The postembryonic shell is ornamented with evenly spaced lirae (Pl. 1, Figs. 1, 2). The lirae are rursiradiate and show a slight adapical sinus on the ventrolateral margin. On the early postembryonic shell the lirae are spaced every 50 µm along the mid-venter. Growth lines are visible between lirae on those parts of the shell not covered by the dorsal wall of the next whorl. The growth lines occur at intervals of 1 µm on the early postembryonic shell (Pl. 1, Fig. 6).

5.2. Outer Wall

The wall of the early postembryonic shell consists of four layers: the inner prismatic layer, the nacreous layer, the outer prismatic layer, and the dorsal wall of the next whorl (Pl. 5, Fig. 4). The inner prismatic layer is extremely thin (thickness equal to one nacreous lamella) but increases in thickness near the umbilical seam and in passing to the dorsum. The outer prismatic layer is relatively thick in comparison with the nacreous layer. In Pl. 5, Fig. 4, the outer prismatic layer is approximately 3.5 µm thick and the nacreous layer is approximately 7 µm thick. During ontogeny, the relative thickness of the outer prismatic layer decreases. The surface of the outer prismatic layer is covered by the dorsal wall of the next whorl.

In cross-section the lirae are visible in the outer prismatic layer (Text-Fig. 3D; Pl. 5, Figs. 3,4). Each lira shows a pattern of discordant prisms, suggesting an interruption in growth.

The thickness of the nacreous plates in the shell wall is 250–300 nm, which is comparable to the thickness of the nacreous plates in the septa. The diameter of the nacreous plates in the shell wall ranges from 4 to 6 µm (Pl. 6, Figs. 1, 2). Plates consist of several sectors, each of which shows a different arrangement of laths (Pl. 6, Figs. 2,3). The laths consist of acicular crystallites with a diameter of 100–150 nm, oriented perpendicular to the surface of the plates (Pl. 6, Fig. 4).

6. Dorsal Wall and Wrinkle Layer

The wrinkle layer first appears on the ventral surface of the initial chamber just adapical of the ammonitella edge (Pl. 2, Fig. 3). The formation of the wrinkle layer at this point presumably corresponds to the secretory zone of the primary varix and is a product of early postembryonic or later embryonic activity. The wrinkle layer does not extend to the umbilical seam (Pl. 1, Figs. 2,3), implying that it does not cover the entire width of the aperture. The dorsal wall of the first whorl of the ammonitella is visible in median cross-section (Pl. 4, Figs. 1–4; Pl. 5, Figs. 1, 2). The outer surface of the ventral wall is flat and is covered by the dorsal wall, which shows wrinkles. The dorsal wall is approximately 2 µm thick between septa 2 and 3 (15 % of the thickness of the ventral wall). The wrinkles show a nearly triangular cross-section. Each wrinkle has a gently sloping adapical face and a more steeply sloping adoral face. The wrinkles are prismatic in microstructure with the prisms oriented perpendicular to the surface of the wall.

The dorsal wall of the second (postembryonic) whorl is smooth without wrinkles (Pl. 1, Figs. 2, 3). In Pl. 7, Figs. 3–6, the dorsal wall is approximately 2 µm thick and displays longitudinal striations on its surface. There is a transverse groove along the crest of each lira separating successive bands of dorsal wall secretion (Pl. 7, Figs. 4, 6). In some areas, the dorsal wall has broken off, revealing the surface of the outer prismatic layer covered with a very thin layer of periostracum (Pl. 7, Fig. 5).

According to Kulicki (1979) and Kulicki et al. (in press), the dorsal wall consists of two components. The outer component is the wrinkle layer and forms in the apertural zone. The inner component is the inner prismatic layer and forms inside the body chamber. The inner prismatic layer covers the wrinkle layer during growth and smoothes out its relief. If the inner prismatic layer is very thin, the relief of the wrinkle layer is visible.

7. Comparison with Other Ammonoids

Because of the extraordinary preservation of these Late Carboniferous goniatites, it is possible to compare them with Mesozoic ammonoids with well preserved shell structure. The ammonitellas of Mesozoic ammonoids display a wide range of variation (see, for example, Branco, 1879–80; Voorthuysen, 1940; Druschits & Doguzhaeva, 1974; Landman et al., 1996). Nevertheless, there are many similarities between the ammonitellas of these goniatites and those of Mesozoic ammonoids. The microstructure of the ammonitella wall is very similar in both groups. There are three layers in the wall of the initial chamber and four layers in the wall of the first whorl of the ammonitella. The microstructure at the ammonitella edge is also the same in both groups (see Kulicki, 1974, Figs. 1,3).

With respect to internal features, the proseptum in these goniatites bears the same relationship to the shell wall as it does in Mesozoic ammonoids (see Kulicki, 1975, 1979; Kulicki & Doguzhaeva, 1994). In addition, the proseptum is prismatic and the second septum is nacreous in both groups. The muscle scar above the flange in these goniatites is also present in Mesozoic ammonoids (see Bandel, 1982, Pl. 17, Fig. 2; Weitschat & Bandel, 1991, Figs. 1,2).

All of these similarities imply a similar mode of embryonic development. They are consistent with the archaeogastropod model proposed by Bandel (1982) and elaborated on by Kulicki & Doguzhaeva (1994). According to this model, the ammonitella initially consisted of an organic shell secreted in direct contact with the gland cells of the mantle. Shortly thereafter, this shell became mineralized forming a thin outer layer. Additional layers were subsequently secreted from the inside, starting backward from the aperture, and served to thicken the original outer layer.

Thus, goniatites shared the same mode of embryonic development as did Mesozoic ammonoids (see also LANDMAN et al., 1999). This conclusion contrasts with earlier interpretations based on less well preserved material (TANABE et al., 1993). Coupled with data from more primitive ammonoids (KLOFAK et al., 1999), these results suggest that all ammonoids followed a similar mode of embryonic development, clearly implying that the ammonitella is a shared derived character of this group.

Nevertheless, there are significant differences between the ammonitellas of these goniatites and those of Mesozoic ammonoids. These differences can be used for phylogenetic analysis and include:

1) The size of the ammonitella angle. The ammonitella angle in goniatites is much larger than that in Mesozoic ammonoids. In goniatites, the ammonitella angle ranges from 345° to 410° compared to a range of 240° to 380° in Mesozoic ammonoids (LANDMAN et al., 1996, Table 1).
2) The shape of the initial chamber. The initial chamber in goniatites is ellipsoidal whereas it is spindle-shaped in Mesozoic ammonoids (BRANCO, 1879–80).
3(The spacing of the first two septa. The first two septa in goniatites are closely spaced on the dorsal side in median cross-section (LANDMAN et al., 1999). Because of their proximity, these two septa have mistakenly been identified in the past as two prosepta (MILLER & UNKLESBAY, 1943). The close spacing of these two septa may be a unique feature of the goniatites although some Mesozoic ammonoids display a somewhat similar condition (DRUSCHITS & DOGUZHAEVA, 1981, Figs. 2–5).
4) The external appearance of the ammonitella. The ammonitellas of these goniatites are smooth without a trace of ornamentation. In contrast, TANABE et al. (1993, Fig. 3) reported longitudinal lirae on the ammonitellas of goniatites from the Upper Carboniferous of Kansas, which are not as well preserved as the Buckhorn Asphalt goniatites. However, new observations suggest that these lirae are part of the dorsal wall (TANABE et al., in prep.). In Mesozoic ammonoids, the ammonitella is covered with a tuberculate ornamentation whereas in more primitive ammonoids such as agoniatites and tornoceratids, the ammonitella is covered with transverse lirae (HOUSE, 1965; LANDMAN et al., 1996; KLOFAK et al., 1999).
5) The dorsal wall and wrinkle layer. In our specimens the wrinkle layer first appears on the ventral surface of the initial chamber and fades out on the early postembryonic shell. KULICKI et al. (in press) have documented wide variation in the morphology and occurrence of the wrinkle layer in Paleozoic and Mesozoic ammonoids. This feature may prove a useful source of information for phylogenetic analysis.

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Plate 1

Goniatitina.
AMNH 46551, Buckhorn Asphalt quarry, Oklahoma, USA.

Fig. 1: Overview showing the ammonitella and part of the postembryonic shell.
The ammonitella is smooth without ornamentation whereas the postembryonic shell is covered with growth lines and evenly spaced lirae. (A small piece of glue is stuck to the initial chamber).
Scale indication = 375 µm.

Fig. 2: Ventral view of the ammonitella and part of the postembryonic shell.
The asterisk indicates the location of Fig. 6.
Abbreviations: AE = ammonitella edge; PC = primary constriction.
Scale indication = 120 µm.

Fig. 3: Ventral view of the ammonitella edge (AE) plastered over by the wrinkle layer.
The wrinkle layer disappears on the postembryonic shell.
Scale indication = 50 µm.

Fig. 4: View of the ammonitella edge near the umbilical seam.
The wrinkle layer is absent.
Scale indication = 30 µm.

Fig. 5: Close-up of the surface of the initial chamber.
It is perfectly smooth without a trace of ornamentation.
Scale indication = 7.5 µm.

Fig. 6: Close-up of the postembryonic shell immediately adoral of the ammonitella edge showing growth lines (arrow).
Scale indication = 15 µm.

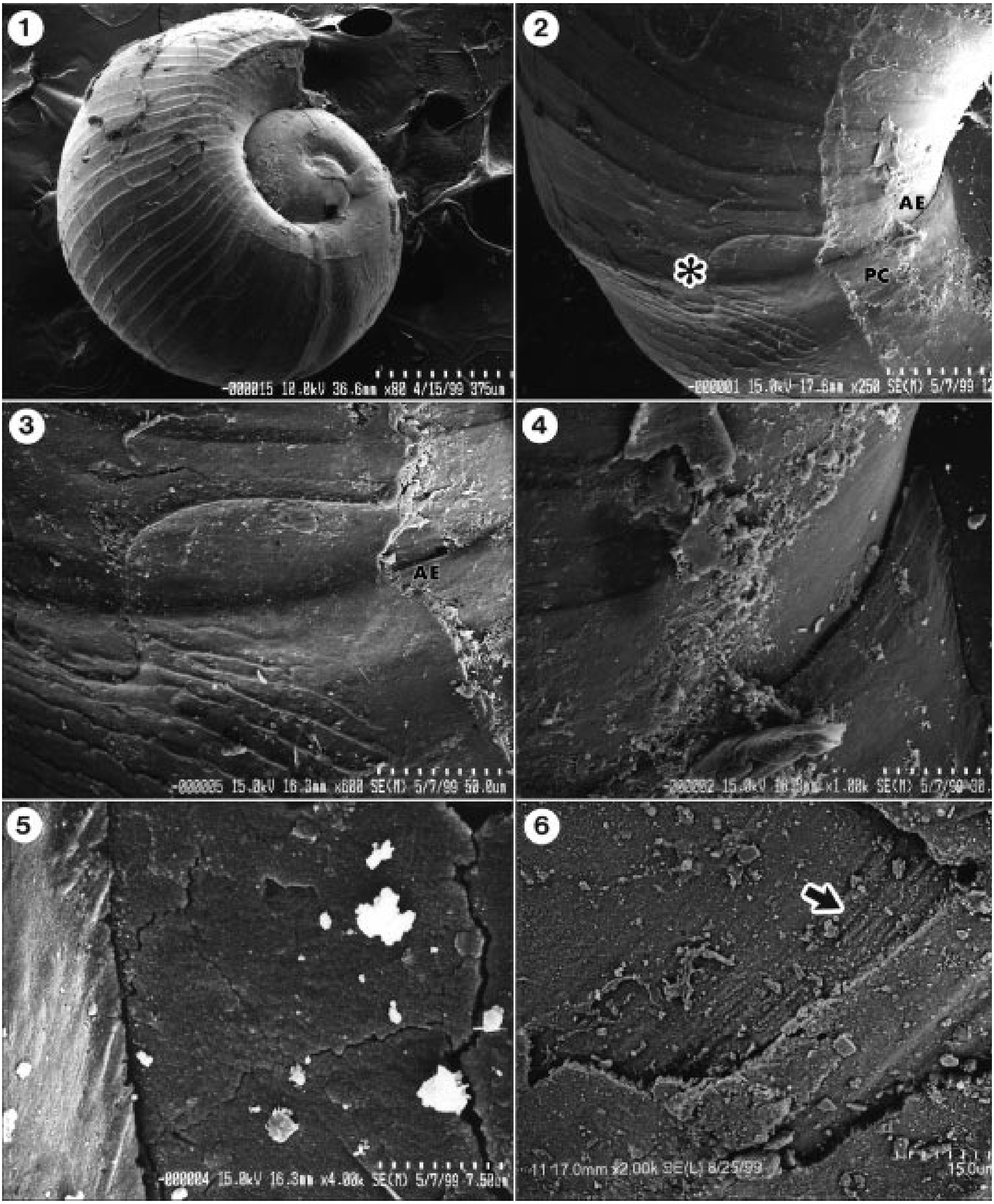

1
2
AE
PC
3
AE
4
5
6

Plate 2

Goniatitina.
AMNH 46552, Buckhorn Asphalt quarry, Oklahoma, USA.

Fig. 1: Overview of a partially broken specimen showing the ammonitella and ammonitella edge (AE).
Scale bar = 200 µm.

Fig. 2: View into the initial chamber showing the flange (F), muscle scar (MS), and proseptum (1) with its central opening.
The caecum and prosiphon are not preserved. The asterisk indicates the location of Fig. 3.
Scale bar = 200 µm.

Fig. 3: Oblique view of the wall of the initial chamber (asterisk in Fig. 2) covered with the wrinkle layer.
Scale bar = 10 µm.

Fig. 4: Close-up of the edge of the wall of the initial chamber showing three layers:
An inner layer representing the mural part of the proseptum (IP), a middle layer, which is the main component of the wall of the initial chamber (WPI), and an outer layer, representing the dorsal wall of the next whorl (DW).
Scale bar = 2 µm.

Fig. 5: Overview of the interior of the initial chamber showing the proseptum (1), flange (F), and muscle scar (MS) above the flange.
Scale bar = 100 µm.

Fig. 6: Close-up of the flange (F) and part of the muscle scar (MS).
Scale bar = 10 µm.

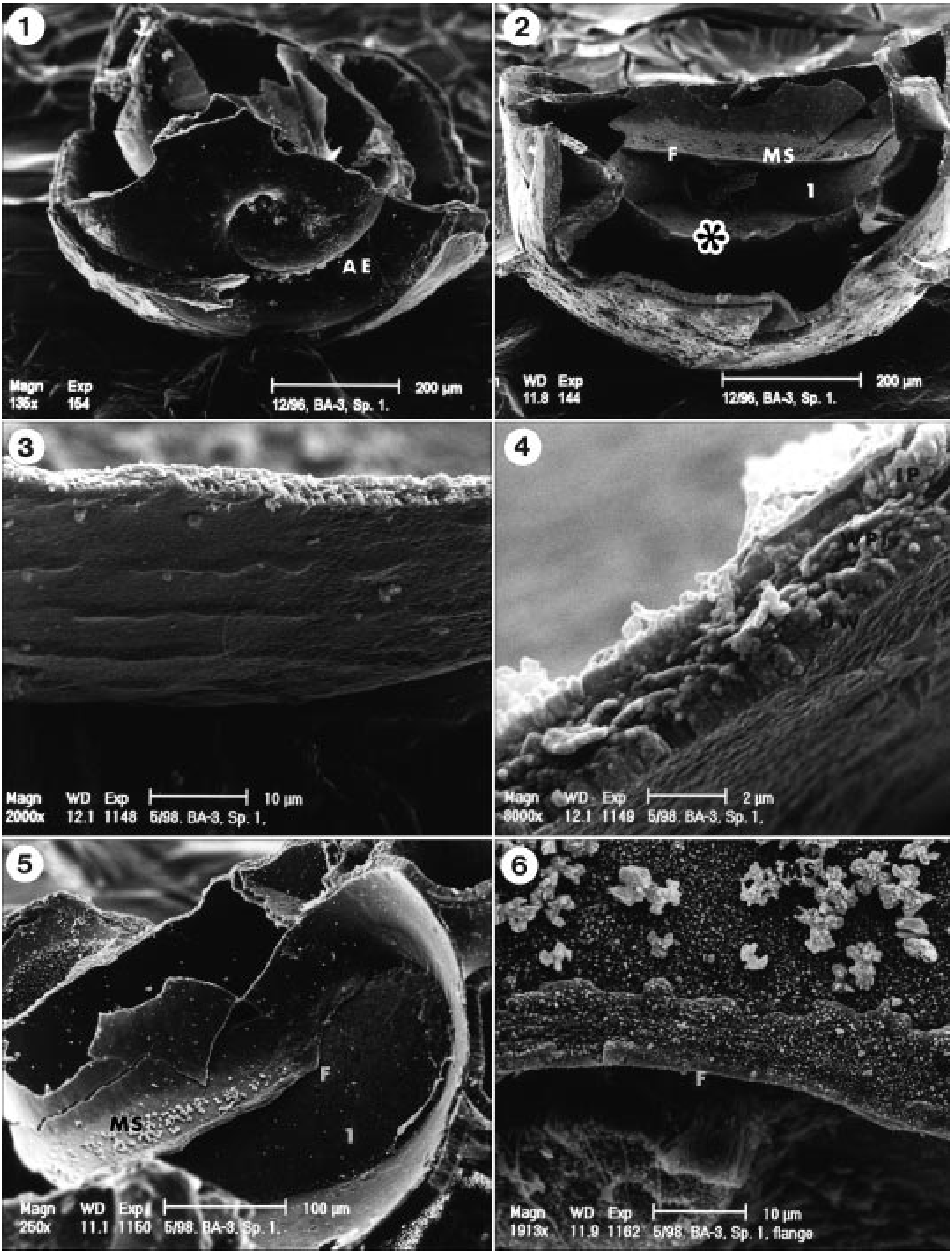

1
AE
Magn Exp
135x 154
200 µm
12/96, BA-3, Sp. 1.
2
F
MS
1
WD Exp
11.8 144
200 µm
12/96, BA-3, Sp. 1.
3
Magn WD Exp
2000x 12.1 1148 5/98. BA-3, Sp. 1,
10 µm
4
IP
Magn WD Exp
8000x 12.1 1149 5/98. BA-3, Sp. 1,
2 µm
5
F
MS
1
Magn WD Exp
250x 11.1 1160 5/98. BA-3, Sp. 1,
100 µm
6
MS
F
Magn WD Exp
1913x 11.9 1162 5/98. BA-3, Sp. 1, flange
10 µm

Plate 3

Goniatitina.
AMNH 46550, Buckhorn Asphalt quarry, Oklahoma, USA.

Fig. 1: Overview showing the ammonitella and part of the postembryonic shell.
Scale bar = 100 µm.

Fig. 2: Median cross-section through the same specimen in the vicinity of the first two septa.
Abbreviations: F = flange; 1 = first septum (proseptum); 2 = second septum.
Scale bar = 50 µm.

Fig. 3: Close-up of the prismatic microstructure of the proseptum.
Scale bar = 2 µm.

Fig. 4: Close-up of the nacreous microstructure of the second septum.
Scale bar = 2 µm.


1
Magn 200x
Exp 179
100 µm
12/96, BA-6, Sp.3
2
1
2
1
2
F
Magn 500x
Exp 241
50 µm
2/07,BA-6,Sp.3, prosepta
3
2 µm
2/07,BA-6,Sp.3;proseptum
4
2 µm
2/07,BA-6,Sp.3, sec. septum

Plate 4

Approximate median cross-section through the early whorls of Goniatitina AMNH 46550. Buckhorn Asphalt quarry, Oklahoma, USA.

Fig. 1: Close-up of the initial chamber in the vicinity of the first septum (proseptum) (1) and second septum (2).
Scale bar = 50 µm.

Fig. 2: Enlargement of the same area showing a secondary calcitic cement (C) covering the surface of the shell.
Scale bar = 20 µm.

Fig. 3: Close-up of the wall of the first whorl between septa 2 and 3.
The adoral direction is toward the top of the photo.
Scale bar = 10 µm.

Fig. 4: Enlargement of the same area showing the inner prismatic layer (IP), wall proper of the ammonitella (WPA), outer prismatic layer (OP), and dorsal wall of the next whorl (DW).
Scale bar = 5 µm.

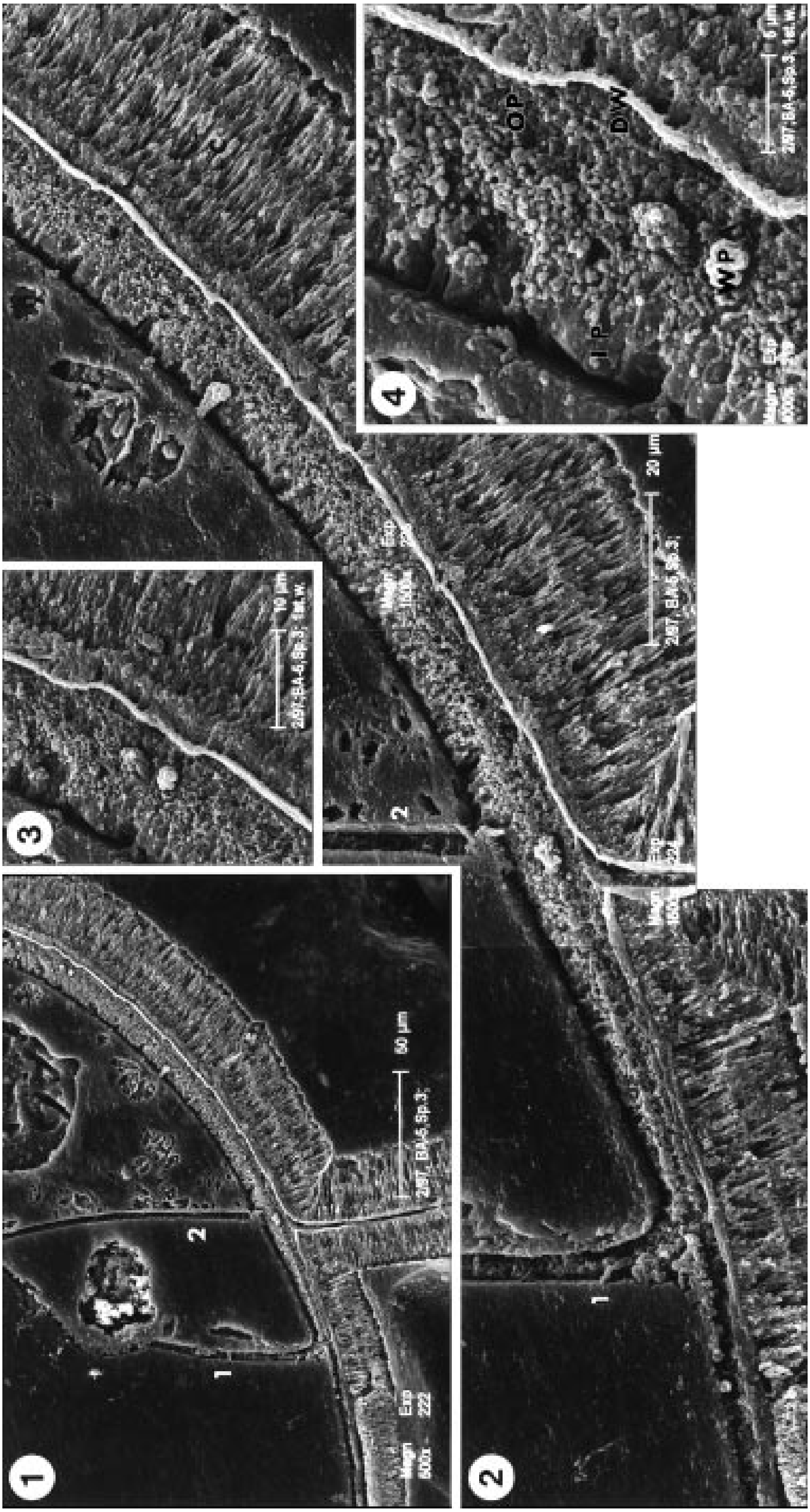

1
2
3
4
OP
DW
WP
50 µm
20 µm
10 µm

Plate 5

Approximate median cross-section through the early whorls of Goniatitina AMNH 46550.
Buckhorn Asphalt quarry, Oklahoma, USA.

Fig. 1: Close-up of the wall of the first whorl.
The adoral direction is toward the upper left.
Scale bar = 20 µm.

Fig. 2: Enlargement of the same area showing the inner prismatic layer (IP), wall proper of the ammonitella (WPA), outer prismatic layer (OP), dorsal wall (DW), and wrinkle layer (WR).
Scale bar = 5 µm.

Fig. 3: Close-up of the wall of the early postembryonic shell showing lirae (L).
The adoral direction is toward the top.
Scale bar = 100 µm.

Fig. 4: Enlargement of the same area at a lira (L).
Abbreviations: DW = dorsal wall; NA = nacreous layer; OP = outer prismatic layer.
Scale bar = 10 µm.

Fig. 5: Close-up of the ammonitella edge.
The adoral direction is toward the left. The left vertical arrow indicates the ammonitella edge; the right vertical arrow, a break in the shell adapical of the edge. The wall of the ammonitella consists of the outer prismatic layer (OP) and the primary varix (PV). The wall of the postembryonic shell consists of an outer prismatic layer (OP) and a nacreous layer (NA). The inner prismatic layer is extremely thin.
Scale bar = 20 µm.

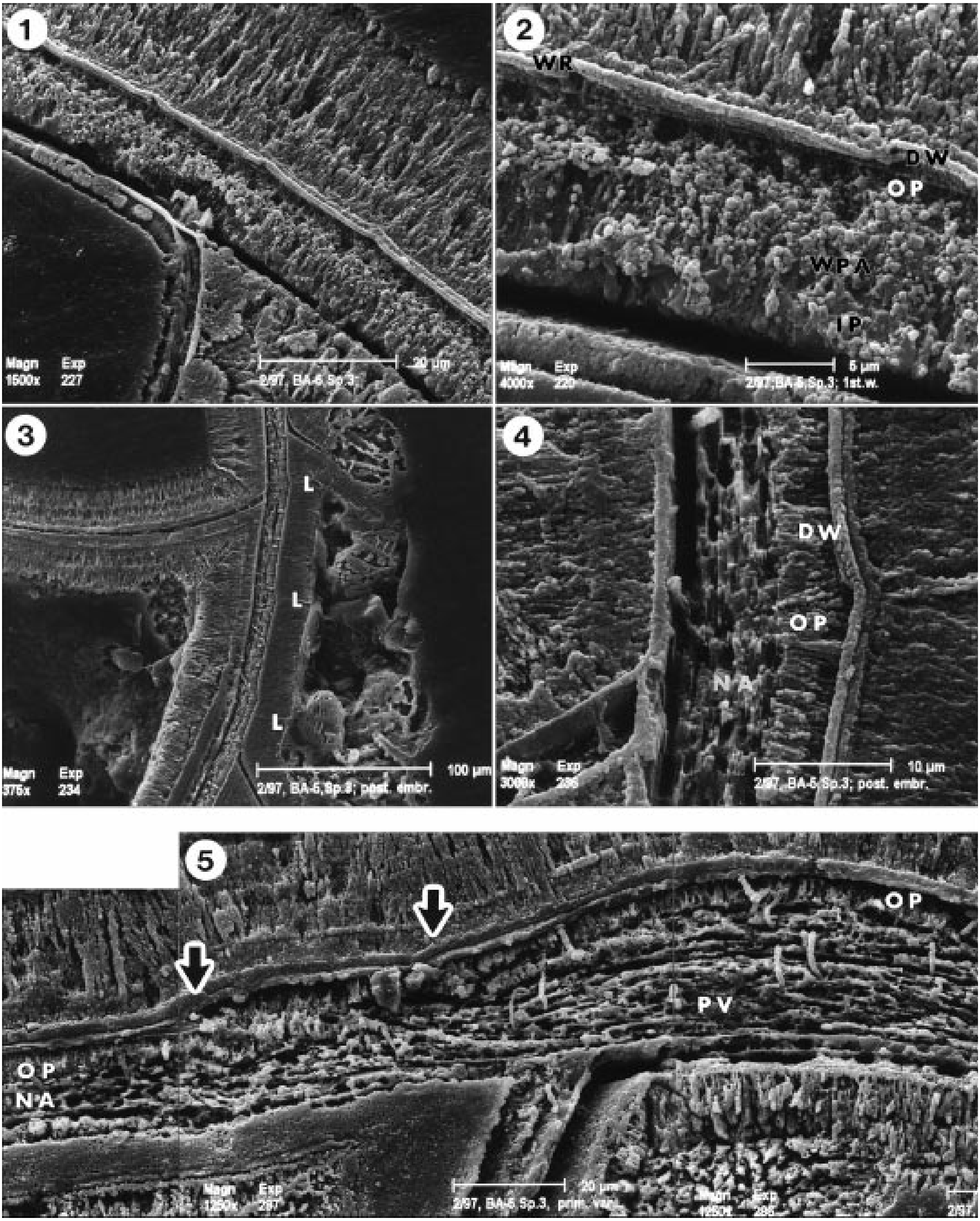

1
Magn Exp
1500x 227
20 µm
2/97, BA-5,Sp.3;
2
WR
DW
OP
WPA
IP
Magn Exp
4000x 220
5 µm
2/97,BA-5,Sp.3; 1st.w.
3
L
L
L
Magn Exp
375x 234
100 µm
2/97, BA-5,Sp.3; post. embr.
4
DW
OP
NA
10 µm
2/97, BA-5,Sp.3; post. embr.
5
OP
PV
OP
NA
20 µm
2/97, BA-5,Sp.3, prim. var.

Plate 6

Close-ups of the nacre in the postembryonic shell of Goniatitina AMNH 46553.
Buckhorn Asphalt quarry, Oklahoma, USA.

Fig. 1: Each nacreous tablet consists of several sectors.
Scale bar = 10 µm.

Fig. 2. The sectors show different arrangements of laths.
Scale bar = 5 µm.

Fig. 3. The laths in each sector are parallel to each other.
Scale bar = 2 µm.

Fig. 4. The laths consist of acicular crystallites oriented perpendicular to the surface of the plates.
Scale bar = 1 µm.

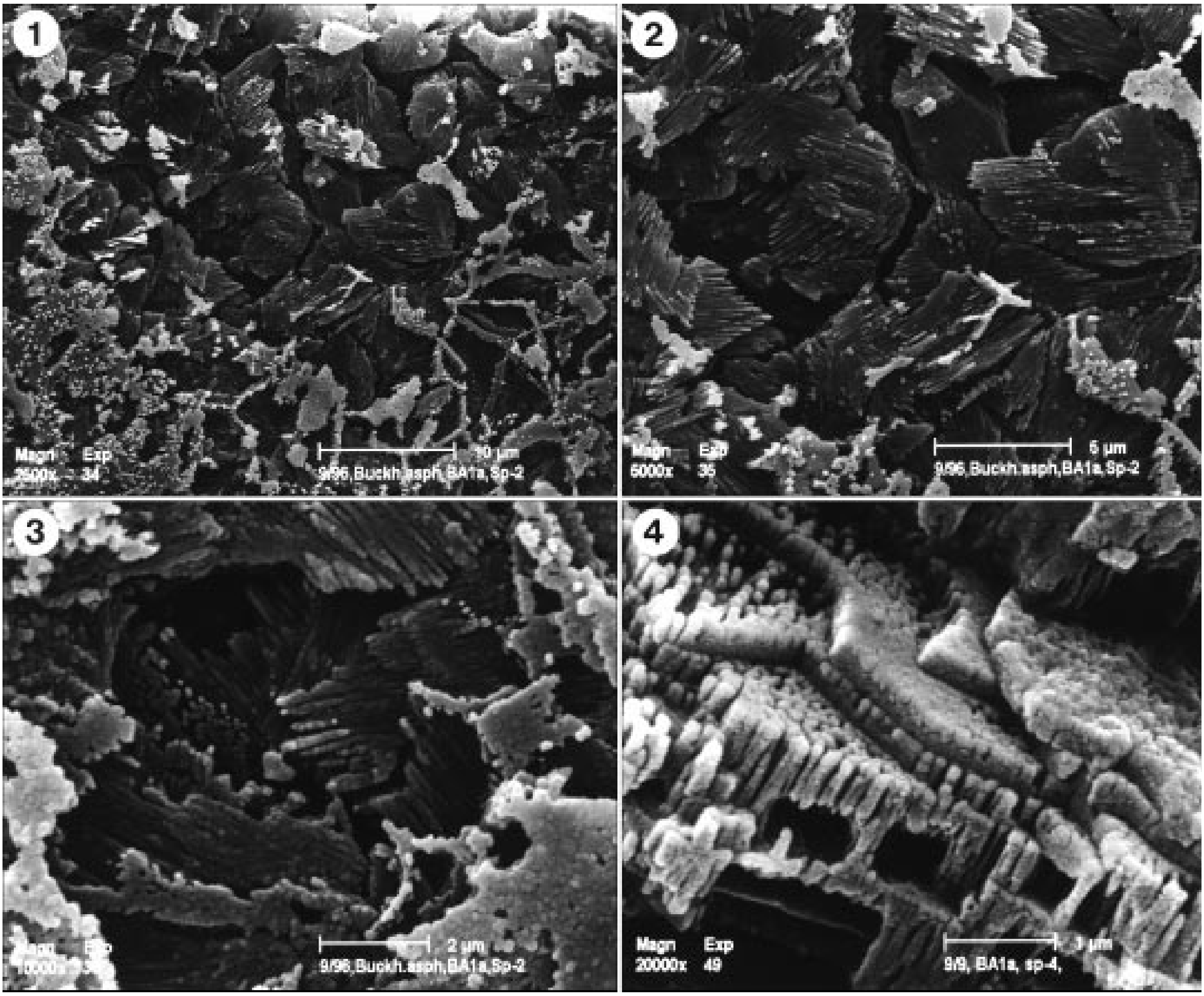

1
Magn Exp
2500x 34
10 µm
9/96,Buckh.asph,BA1a,Sp-2
2
Magn Exp
5000x 35
5 µm
9/96,Buckh.asph,BA1a,Sp-2
3
2 µm
9/96,Buckh.asph,BA1a,Sp-2
4
Magn Exp
20000x 49
1 µm
9/9, BA1a, sp-4,

Plate 7

Views of the dorsal wall and wrinkle layer in the Goniatitina.
Buckhorn Asphalt quarry, Oklahoma, USA.

Fig. 1: Overview of a fragment of the ammonitella showing the primary constriction (PC).
The adoral direction is toward the left.
AMNH 46554.
Scale bar = 100 µm.

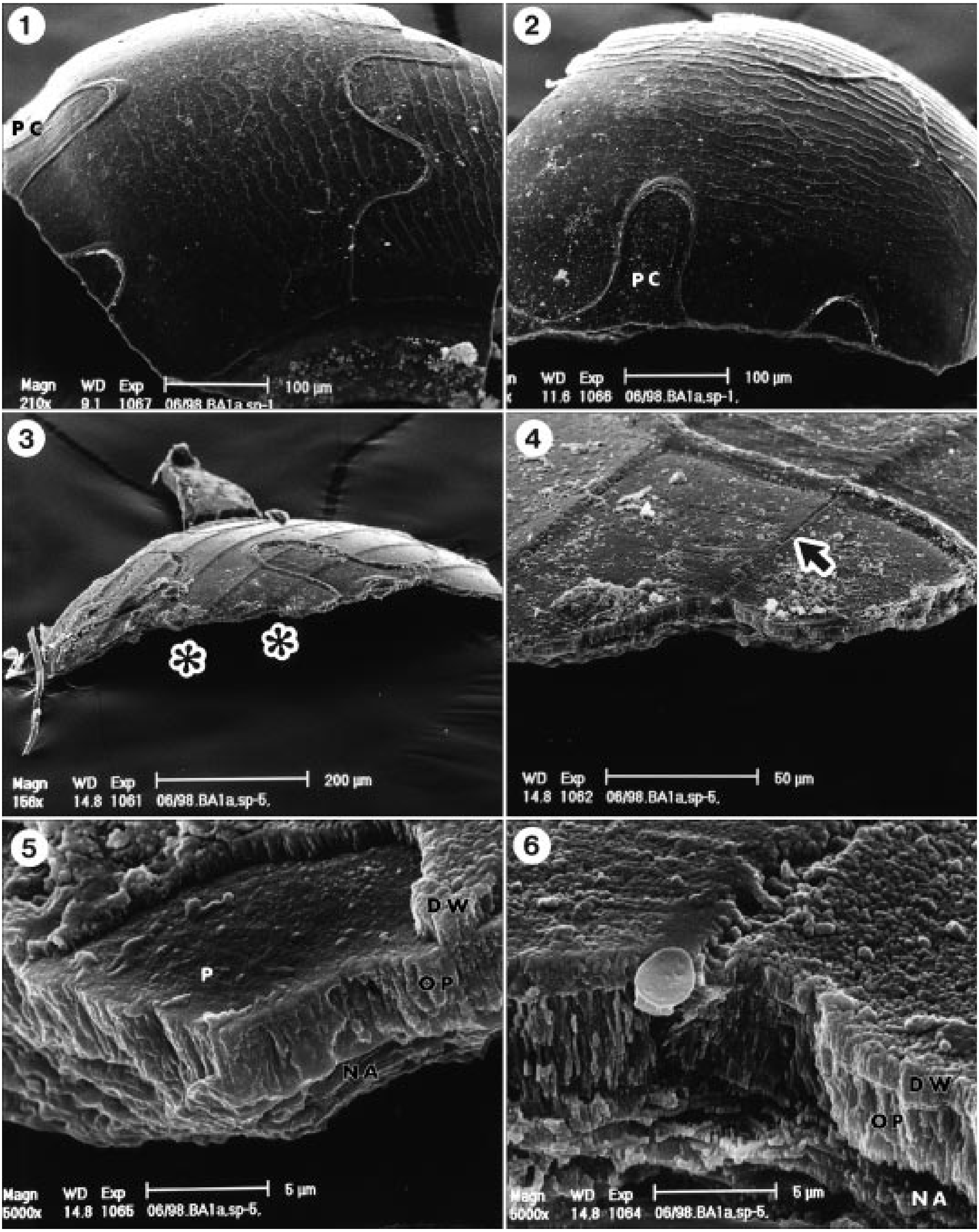
Fig. 2: The wrinkles disappear near the primary constriction (PC).
AMNH 46554.
Scale bar = 100 µm.

Fig. 3: Overview of a fragment of the postembryonic shell, probably from the second whorl.
The adoral direction is toward the lower right. The asterisks indicate the locations of Figs. 5 and 6.
AMNH 46555.
Scale bar = 200 µm.

Fig. 4: The surface of the dorsal wall does not show wrinkles.
The transverse groove (arrow) is developed in the dorsal wall above a lira.
AMNH 46555.
Scale bar = 50 µm.

Fig. 5: Close-up of the edge of the shell (left asterisk in Fig. 3) showing the dorsal wall (DW), outer prismatic layer (OP), and nacreous layer (NA). Part of the dorsal wall has broken off exposing the surface of the outer prismatic layer covered with a thin layer of periostracum (P).
AMNH 46555
Scale bar = 5 µm.

Fig. 6: Close-up of the edge of the shell (right asterisk) showing the dorsal wall (DW), outer prismatic layer (OP), and nacreous layer (NA).
AMNH 46555.
Scale bar = 5 µm.


1
PC
Magn WD Exp 100 µm
210x 9.1 1067 06/98.BA1a.sp-1
2
PC
WD Exp 100 µm
11.6 1066 06/98.BA1a.sp-1.
3
Magn WD Exp 200 µm
156x 14.8 1061 06/98.BA1a.sp-5.
4
WD Exp 50 µm
14.8 1062 06/98.BA1a.sp-5.
5
DW
P
OP
NA
Magn WD Exp 5 µm
5000x 14.8 1065 06/98.BA1a.sp-5.
6
DW
OP
NA
Magn WD Exp 5 µm
5000x 14.8 1064 06/98.BA1a.sp-5.

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