Micro-ornamentation on the embryonic and postembryonic shells of Triassic ceratites (Ammonoidea)

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Abstract: The ceratites *Trachyceras (Trachyceras) aon* (Münster, 1834) and related species in the family Trachyceratidae from the Upper Triassic (lower Carnian) San Cassiano Formation of Italy display a tuberculate micro-ornamentation on their embryonic shells (ammonitellas). The tubercles are irregularly distributed over the exposed portions of the ammonitella and terminate at the ammonitella edge. The tubercles are approximately 4 μm in diameter and are extensions of pseudohexagonal trillings in the outer prismatic layer of the shell wall. This micro-ornamentation is similar to that on the ammonitellas of other Mesozoic ammonoids including Phylloceratina, Ammonitina, Ancyloceratina, and Lytoceratina, and different from that on the ammonitellas of Paleozoic ammonoids including Agoniatitina, Anarcestina, Tornoceratina, and Goniatitina. The presence of this tuberculate micro-ornamentation may represent a synapormorphy for Mesozoic ammonoids.

These ceratites also display a micro-ornamentation on their postembryonic shells consisting of tubercles and ridges aligned in longitudinal rows. This micro-ornamentation has been observed in several species of Jurassic ammonites and bears some resemblance to the wrinkle layer. However, unlike the wrinkle layer, it probably formed at the growing edge of the mantle and reflected the ornamentation of the periostracum.

Key Words: ammonoids, Triassic, embryonic shell, micro-ornamentation

The micro-ornamentation on the embryonic shell (ammonitella) of ammonoids has been described in several suborders including the Agoniatitina, Anarcestina, and Tornoceratina, where it consists of transverse lirae, in the Lytoceratina, Ancyloceratina, Phylloceratina, and Ammonitina, where it consists of tubercles, and in the Goniatitina in which the ammonitella is smooth (see the recent review by Landman *et al.*, 1996; for goniatites, see Kulicki *et al.*, in press,b). In this paper, we describe for the first time the micro-ornamentation on the ammonitellas of ceratites and comment on the phylogenetic implication of this finding. We also document the micro-ornamentation on the postembryonic shells of these species.

MATERIAL AND METHODS

The ceratites studied belong to *Trachyceras (Trachyceras) aon* (Münster, 1834), *T. (T.) muensteri* (Wissmann, 1841), *T. (Brotheotrachyceras) larva* (Klipstein, 1843), and related species in the family Trachyceratidae. The specimens are from the Upper Triassic (lower Carnian) San Cassiano (= St. Cassian) Formation of Prati di Stuores in the Italian Dolomites (see Figs. 1 and 2 for a map of the region and a generalized stratigraphic section, respectively). The ammonoids and other faunal elements of this formation have been extensively studied because of their superb preservation (see Urlichs, 1974, 1994; Bizzarini, 1988, 1996; Bizzarini and Braga, 1987; Bizzarini and Gnoli, 1991; Bizzarini *et al.*, 1986; Bandel, 1994; Neri *et al.*, 1995; Stanley and Swart, 1995). The ceratites at our disposal are pyritized steinkerns with parts of their original aragonitic shell preserved.

Specimens were mechanically broken down using needles and snippers and selected fragments were then mounted on stubs for scanning electron microscopy (SEM). The terminology of the ammonitella is reviewed in Landman *et al.* (1996). Approximately 15 specimens were examined, six of which are described in this paper. They are reposited in the American Museum of Natural History (AMNH) and the Museo Civico di Storia Naturale di Venezia (MCSNV).

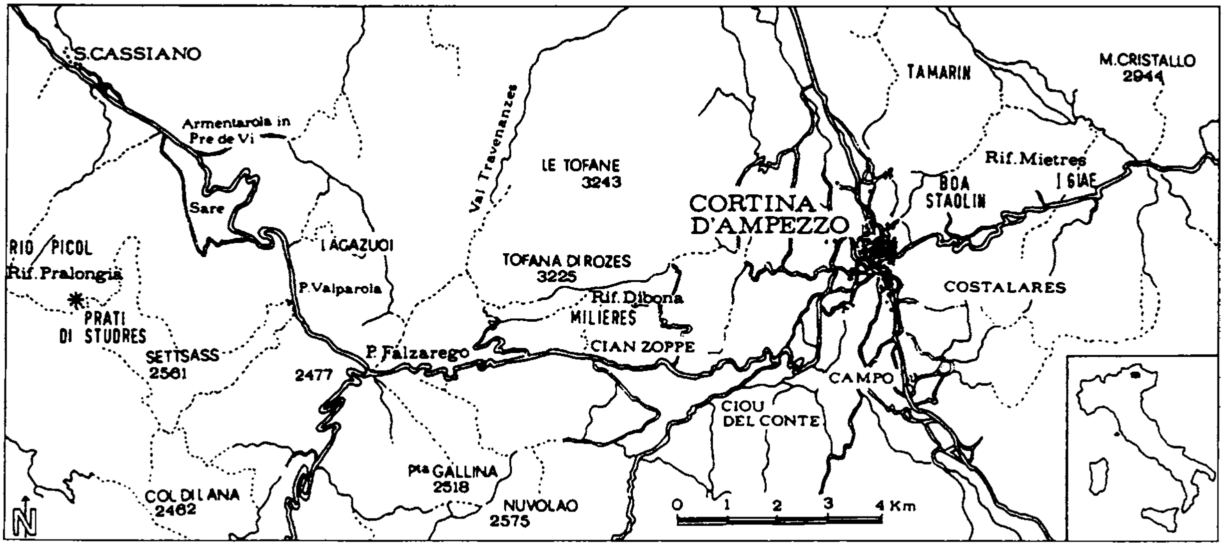

Fig. 1. Map of the general area in Italy in which the specimens were collected (elevations in meters). The best preserved material comes from Prati di Stuores (asterisk, western edge of the map).

RESULTS

The ceratites studied display a tuberculate micro-ornamentation on their ammonitellas. The tubercles are approximately 4 µm in diameter and disappear at the ammonitella edge. This micro-ornamentation is illustrated in AMNH 46594-46597.

AMNH 46594, *Trachyceras* cf. *Trachyceras (T.) aon*, preserves a small patch of outer shell on the first whorl of the ammonitella (Fig. 3A). At high magnifications (500x, 1000x), tubercles are visible on the shell surface (Fig. 3B, C). They are irregularly distributed, although it is not uncommon for three or four tubercles to form a short row (Fig. 3C). The tubercles are approximately 4 µm in diameter and 2 µm in height (Fig. 3D-F).

The wall of the ammonitella appears to consist of three prismatic layers, which total approximately 11 µm in thickness (Fig. 3D). The outermost layer is 1-2 µm thick. The prisms in this layer are approximately 1.5 µm in diameter and seem to be arranged in longitudinal rows (Fig. 3C). These prisms are organized into larger units, approximately 4 µm in diameter, which represent pseudohexagonal trillings (= three cyclically twinned crystals forming a hexagon) (Fig. 3E, F). The tubercles are extensions of the pseudohexagonal trillings and are composed of multiple sectors (Fig. 3E, F).

In AMNH 46595, *Trachyceras (Brotheotrachyceras) larva*, part of the shell wall is preserved at the primary constriction (Fig. 4A). Tubercles are visible on the adapical side of the deepest part of the constriction (Fig. 4B, C). They are approximately 4 µm in diameter (Fig. 4D). They are sparsely and irregularly distributed and are part of the

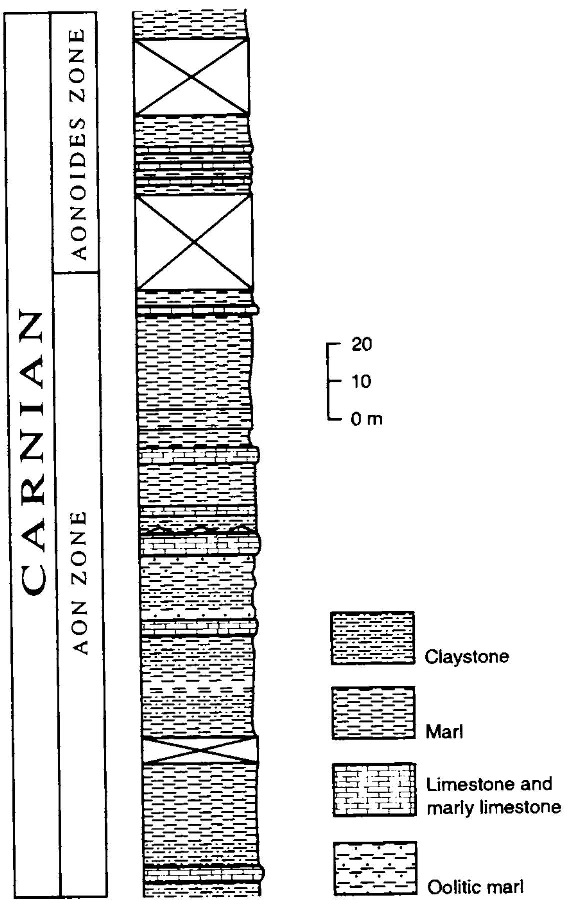

Fig. 2. Generalized stratigraphic section of the Upper Triassic (Carnian) San Cassiano Formation at Prati di Stuores. The ammonites studied occur throughout the section. The Aon and Aonoides Zones are ammonite biozones.

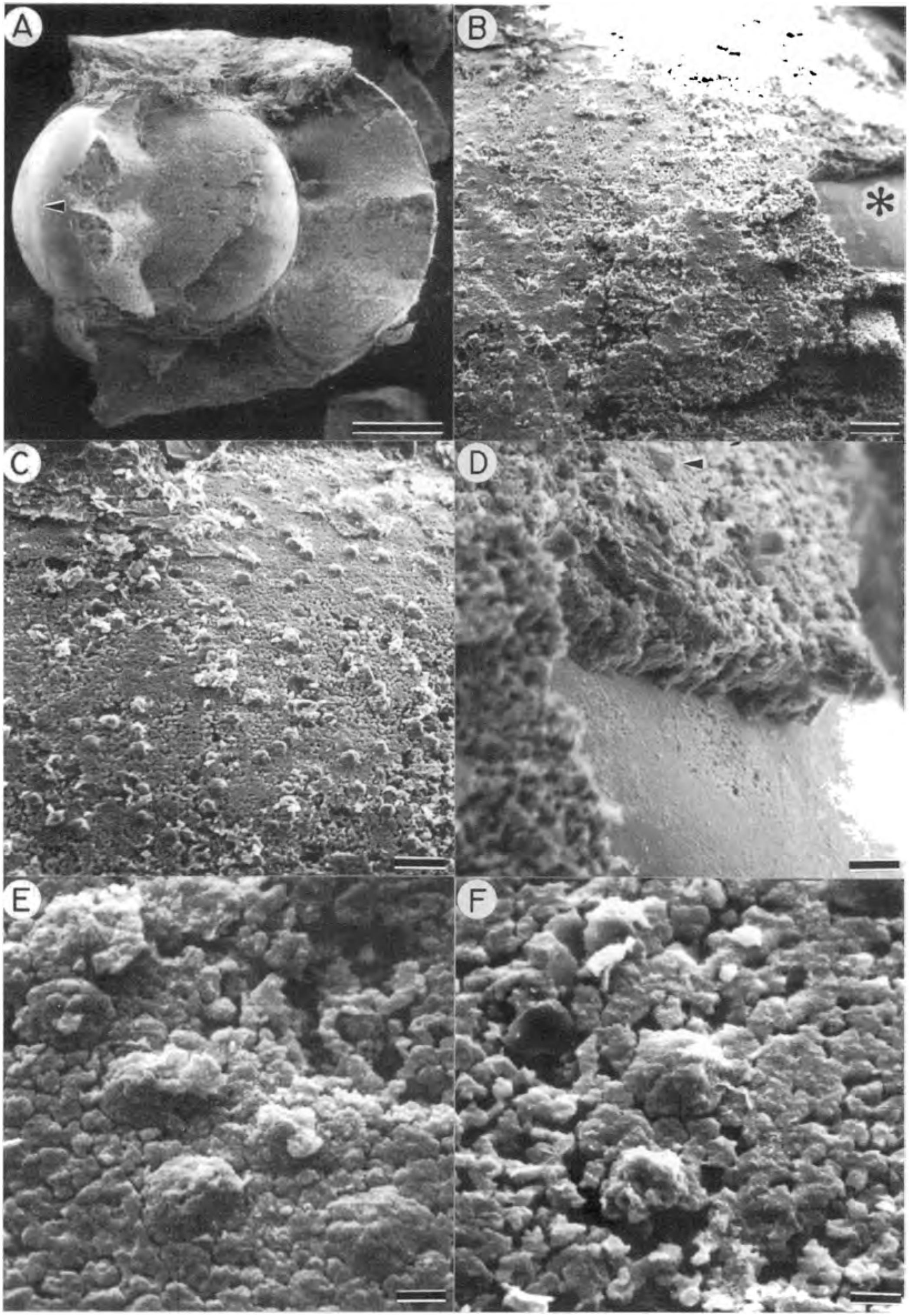

Fig. 3. *Trachyceras* cf. *Trachyceras (T.) aon* (Münster, 1834), AMNH 46594, San Cassiano Formation, Dolomites, Italy. A. Ventral view of the first whorl of the ammonitella and the primary constriction (arrow). Scale bar = 200 μm. B. Close-up of a patch of shell with tubercles. The adoral direction is toward the right. The asterisk indicates the position of D. Scale bar = 20 μm. C. The tubercles are densely and randomly distributed. Note the longitudinal arrangement of the prismatic crystals. Scale bar = 10 μm. D. Close-up of a broken part of the shell wall showing three prismatic layers. The outermost layer is covered with tubercles (arrow). Scale bar = 5 μm. E. The tubercles are extensions of pseudohexagonal trillings. Scale bar = 2 μm. F. The outer layer is composed of prismatic crystals oriented perpendicular to the surface. Scale bar = 2 μm.

outer prismatic layer. A nacreous layer is visible at some depth below the outer prismatic layer and represents the nacre of the primary varix (Fig. 4C).

AMNH 46596, *Trachyceras (Trachyceras) aon*, also preserves a patch of shell wall on the ammonitella near the primary constriction (Fig. 5A). The shell is covered with irregularly distributed tubercles (Fig. 5B). The prisms of the outer layer are visible on the shell surface, especially where the surface is eroded (Fig. 5C, left side). The tubercles are approximately 4 µm in diameter and are composed of multiple sectors converging to a conical top (Fig. 5D). In some areas, the tubercles are missing, leaving depressions in the outer layer (Fig. 5D, right side). The tubercles become slightly smaller and disappear near the end of the primary constriction (Fig. 5E, F).

The best specimen is AMNH 46597, *Trachyceras (Trachyceras) aon*. Tubercles cover the entire exposed surface of the ammonitella but are better developed on the first whorl than on the initial chamber (Fig. 6A). The tubercles are densely and irregularly distributed (Fig. 6A-C). Each tubercle is approximately 4 µm in diameter with an hexagonal outline (Fig. 6D). The tubercles disappear at the

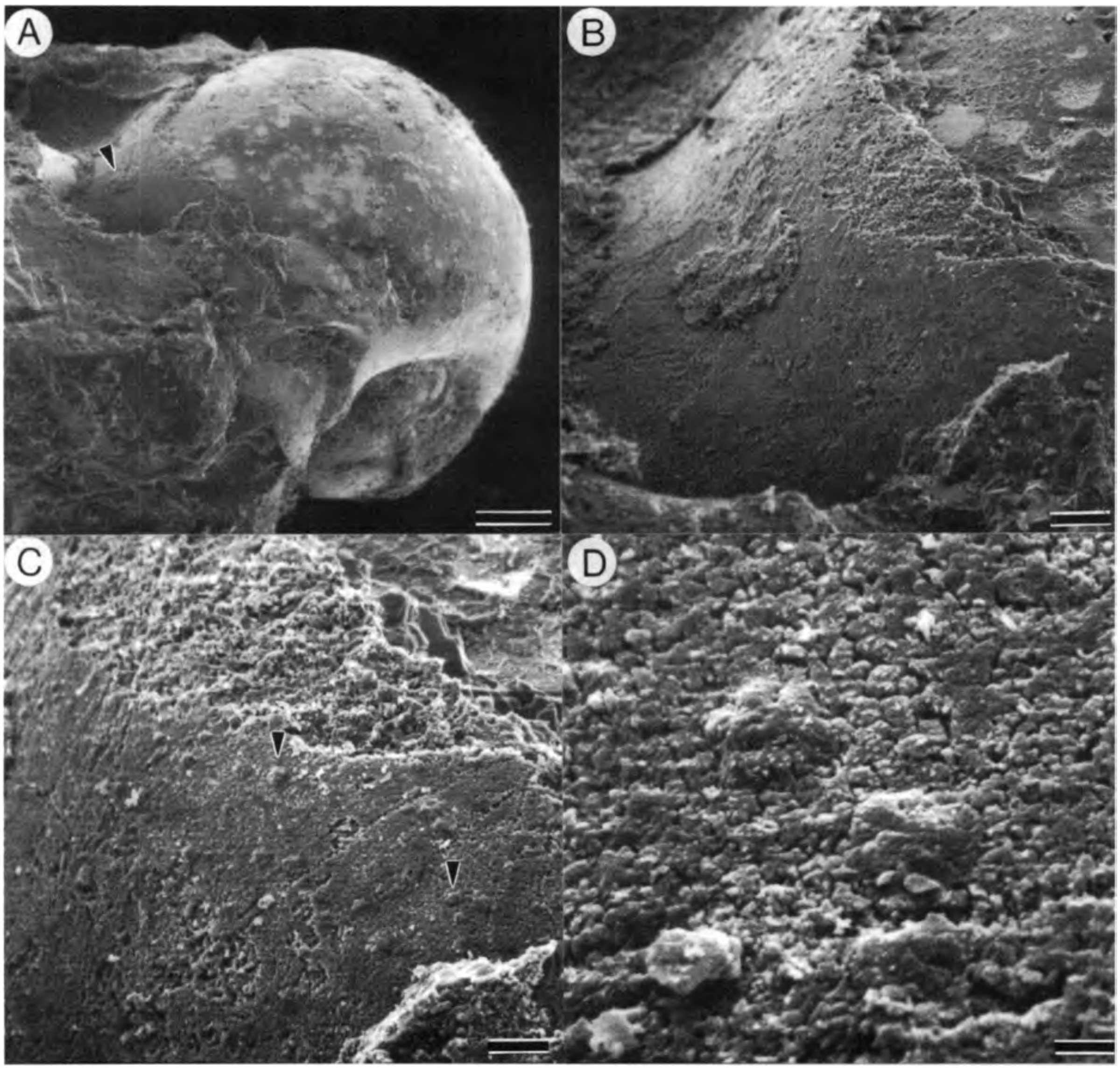

Fig. 4. *Trachyceras (Brotheotrachyceras) larva* (Klipstein, 1843), AMNH 46595, San Cassiano Formation, Dolomites, Italy. A. Ventral view of the adoral end of the ammonitella showing the primary constriction (arrow). Scale bar = 100 µm. B. Close-up of the primary constriction. Scale bar = 20 µm. C. The tubercles (arrows) are visible on the adapical part of the primary constriction. Scale bar = 10 µm. D. Close-up of the tubercles, which appear to be extensions of pseudohexagonal trillings. Scale bar = 2 µm.

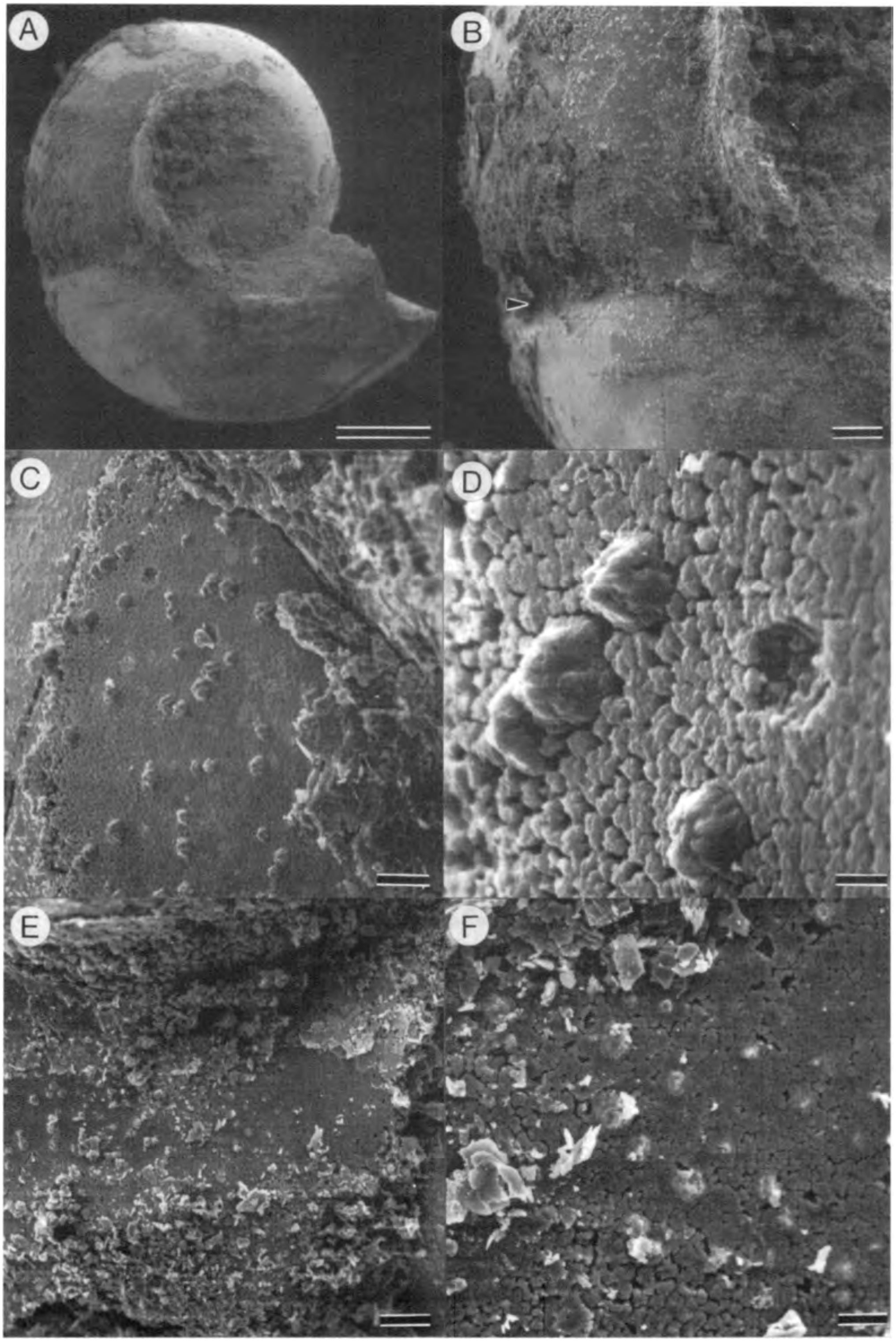

Fig. 5. *Trachyceras (Trachyceras) aon* (Münster, 1834), AMNH 46596, San Cassiano Formation, Dolomites, Italy. A. Right lateral view of the ammonitella and part of the first whorl. Scale bar = 200 μm. B. A patch of shell is visible on the adoral end of the ammonitella near the primary constriction (arrow). Scale bar = 50 μm. C. The tubercles are irregularly distributed on the shell surface. The specimen has been rotated 30° clockwise relative to A. Scale bar = 10 μm. D. The tubercles are composed of multiple sectors converging to a conical top. Scale bar = 2 μm. E. Close-up of the shell surface at the primary constriction. The adoral direction is toward the right (same orientation as C, D). Scale bar = 20 μm. F. The tubercles disappear in the adoral direction (toward the right) in the primary constriction. Scale bar = 5 μm.

ammonitella edge, which is very well defined in this specimen (Fig. 6E, F). The postembryonic shell shows a series of discontinuous, transverse lirae composed of interconnected tubercles (Fig. 6E, left arrow).

Micro-ornamentation is also present on the postembryonic whorls of these ceratites and consists of ridges and tubercles aligned in longitudinal rows. This micro-ornamentation is illustrated in AMNH 46598 and AMNH 46599.

In AMNH 46598, *Trachyceras* cf. *Trachyceras (T.) aon*, there is a piece of the postembryonic shell wall on the left side of the specimen (Fig. 7A). Micro-ornamentation covers the whole flank from one umbilical seam to the other, but is less distinct on the inner two thirds of the flank than on the outer one third of the flank (Fig. 7B). The micro-ornamentation consists of ridges and tubercles arranged in longitudinal rows. The ridges and tubercles form a broad concavity on the inner two-thirds of the flank and are straight and prorsiradiate on the outer one third of the flank. The ridges and tubercles occur on a porous spicular surface. Large crystallites are visible where this surface is eroded (Fig. 7C, lower left). The surface is free of growth lines (Fig. 7C) although faint ribs and a marked growth discontinuity (Fig. 7B, asterisk) are present on the outer flank.

There is some variation in the shape of the ridges and tubercles on the postembryonic shell. Some elements are symmetric but most have an asymmetric profile with a steeply sloping adoral face and a more gently sloping adapical face. The tubercle on the right side in Fig. 7D is approximately 10 μm in length.

The micro-ornamentation on the postembryonic shell is beautifully preserved in AMNH 46599, *Trachyceras (Trachyceras) muensteri* (Fig. 8). This specimen consists of half a postembryonic whorl broken off of a larger specimen. The ammonitella is completely covered up. On the adapical end of the fragment, the micro-ornamentation is present on a patch of outer shell and extends from the umbilical seam to the right side of the mid-venter (Fig. 8A). The micro-ornamentation consists of tubercles and ridges aligned in longitudinal rows (Fig. 8A, B). The tubercles and ridges follow a prorsiradiate pattern on the outer flanks.

The tubercles are asymmetric in shape and seem to be composed of several sectors. They are approximately 8 μm in diameter and approximately 4 μm in height (Fig. 8C, left side). They are developed on a thin prismatic layer approximately 2 μm thick. The prismatic crystals composing this layer seem to be organized into pseudohexagonal trillings (Fig. 8C, upper right). Growth lines are absent although viewed from a low angle, the surface shows a series of undulations, each approximately 10 μm in width, oriented perpendicular to the direction of growth (Fig. 8A).

On the adoral portion of this specimen, micro-ornamentation is preserved on the venter and flanks (Fig. 8D). It consists of ridges and tubercles aligned in longitudinal rows (Fig. 8E). The individual ridges are elongated in a longitudinal direction; the ridge in Fig. 8F is 20 μm long.

DISCUSSION

The ammonitellas of these ceratites are covered with tubercles, each approximately 4 μm in diameter. The tubercles occur on the exposed portions of the ammonitella and disappear at the ammonitella edge. They seem to be extensions of pseudohexagonal trillings in the outer prismatic layer. They form an integral part of this layer as indicated by the presence of depressions where individual tubercles have broken off (Fig. 5D).

The shape, size, distribution, and microstructure of these tubercles indicate that they are homologous to those reported on the ammonitellas of other Mesozoic suborders, namely Lytoceratina, Phylloceratina, Ancyloceratina, and Ammonitina, known collectively as the Ammonitida (see, for example, Brown, 1892, pl. 9, fig. 4; Kulicki, 1974, pl. 4, fig. 1; Kulicki, 1979, pl. 48, fig. 3; Kulicki, 1996, figs. 4D, 5E, F; Kulicki and Doguzhaeva, 1994, fig. 11D, F; Bandel, 1982, pl. 13, figs. 1, 6, 7; Bandel *et al.*, 1982, figs. 1, 2; Landman, 1985, fig. 2B; Landman, 1987, fig. 4; Landman, 1988, fig. 1; Landman, 1994, figs. 2, 3; Landman and Waage, 1993, figs. 13, 14; Landman *et al.*, 1996, figs. 12, 13; Tanabe, 1989, figs. 1-3, 4C, D; Sprey, in press, fig. 3A). This micro-ornamentation differs from that on the ammonitellas of Paleozoic ammonoids, which are covered by transverse lirae in the Agoniatitina, Anarcestina, and Tornoceratina, and are smooth in the Goniatitina (Landman *et al.*, 1996; for goniatites, see Kulicki *et al.*, in press, b). The presence of the same micro-ornamentation on the ammonitellas of Mesozoic ammonoids may represent a synapomorphy for this group.

The size and morphology of the tubercles vary slightly among Mesozoic ammonoid suborders, possibly providing useful characters for phylogenetic analysis. In the Ceratitina, the tubercle size averages 4 μm based on several specimens of *Trachyceras*. In the Ammonitina, the tubercle size ranges from 2-4 μm based on a sample of seven genera (*Anapachydiscus, Metaplacenticeras, Desmophyllites, Quenstedtoceras, Kosmoceras, Aconeceras*, and *Binatisphintes*) (see above references). In the Phylloceratina, the tubercle size averages 3 μm in a single specimen of *Hypophylloceras* (see Tanabe, 1989, fig. 2D). In contrast, the tubercle size is larger in the Lytoceratina and Ancyloceratina. It ranges from 3.5-7 μm in two genera of Lytoceratina (*Gaudryceras* and *Anagaudryceras*), and 4.5-7.5 μm in five genera of Ancyloceratina (*Scaphites, Hoploscaphites, Clioscaphites, Jeletzkytes*, and *Discoscaphites*) (see above references).

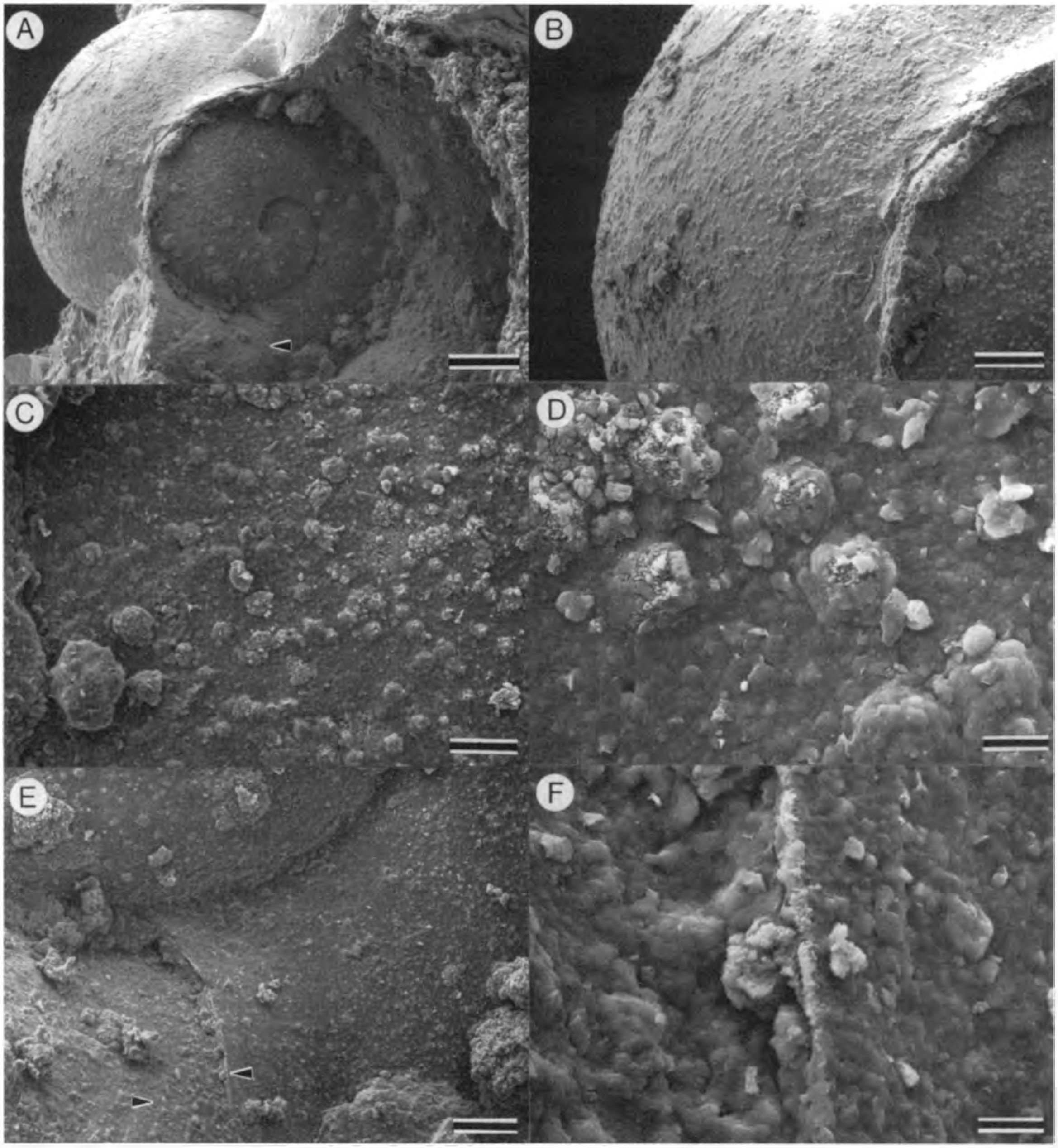

Fig. 6. *Trachyceras (Trachyceras) aon* (Münster, 1834), AMNH 46597, San Cassiano Formation, Dolomites, Italy. A. The postembryonic whorls have broken off exposing the ammonitella and ammonitella edge (arrow). The remnant of the umbilical seam of the succeeding whorl is still attached. Scale bar = 115 µm. B. The ammonitella is covered with tubercles. Scale bar = 50 µm. C. The tubercles are densely and irregularly distributed on the shell surface. Scale bar = 15 µm. D. Close-up of the tubercles. Scale bar = 3 µm. E. The ammonitella edge (right arrow) is sharply defined. Note the micro-ornamentation (left arrow) on the postembryonic shell. Scale bar = 30 µm. F. Close-up of the ammonitella edge. Scale bar = 3 µm.

Another source of variation is the distributional pattern of tubercles on the shell surface, but it is difficult to determine how much of this variation is due to differences in preservation. For example, Tanabe (1989, fig. 2C) noted in some species that the density of tubercles on the first whorl of the ammonitella is greater nearer the umbilical seam with the next whorl than on the rest of the flanks. Tanabe (1989, fig. 1A) also noted that tubercles sometimes form a continuous layer on the umbilical wall of the initial chamber even though they are distinct on the rest of the ammonitella. In our ceratites, the tubercles are generally uniformly distributed on the shell surface, although in AMNH 46597, the tubercles are less densely distributed on the initial chamber than on the first whorl.

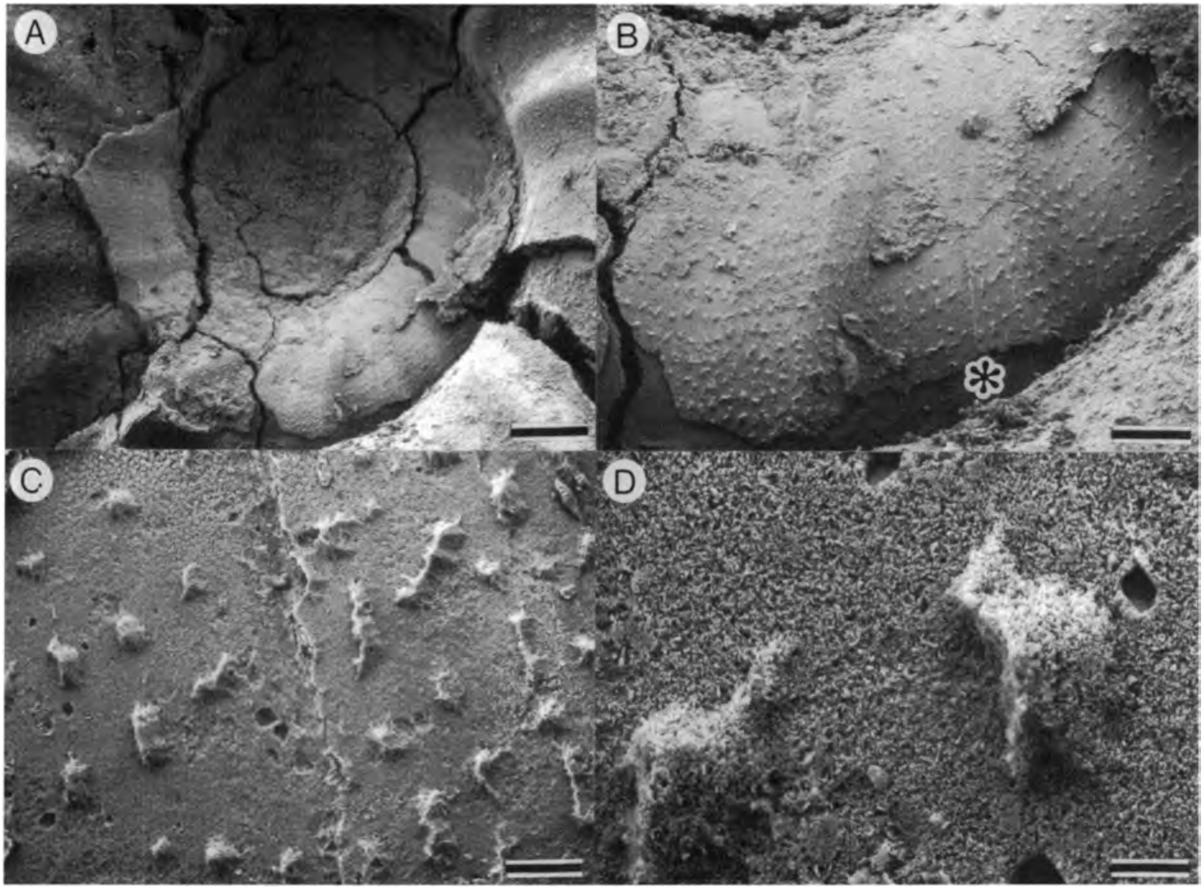

Fig. 7. *Trachyceras* cf. *Trachyceras (T.) aon* (Münster, 1834), AMNH 46598, San Cassiano Formation, Dolomites, Italy. A. Overview of the early postembryonic whorls. The ammonitella is not exposed. Scale bar = 215 µm. B. The micro-ornamentation consists of tubercles and ridges aligned in longitudinal rows. Note the growth discontinuity (asterisk). Scale bar = 75 µm. C. Close-up of tubercles and the growth discontinuity. The adoral direction is toward the left. Scale bar = 15 µm. D. The tubercle on the right has an asymmetric profile with a gently sloping adapical face and a more steeply sloping adoral face. The adoral direction is toward the left. Scale bar = 3 µm.

A further source of variation is tubercle microstructure, although this variation, again, might principally be due to differences in preservation. For example, the tubercles in scaphitid ammonoids appear to be monolithic (see, for example, Tanabe, 1989, figs. 2D, 3A; Landman and Waage, 1993, fig. 13F) whereas those in other ammonoids such as *Quenstedtoceras* are clearly composed of multiple sectors (see Bandel *et al.*, 1982, fig. 2C). In most of our specimens of *Trachyceras*, the tubercles are extensions of pseudohexagonal trillings in the outermost prismatic layer and consist of multiple sectors (Fig. 3F).

The absence of growth lines on the surface of all ammonitellas indicates that the embryonic shell was secreted in uninterrupted contact with the gland cells of the mantle. However, the mode of formation of the tubercles is still unknown. There are two competing hypotheses. Bandel (1982, 1986) suggested that the ammonitella of Mesozoic ammonoids initially consisted of an organic, unmineralized shell with tubercles. He argued that this shell was mineralized by prismatic needles from the inside, preserving its original micro-ornamentation. Tanabe (1989) proposed an alternative model in which the mode of embryonic development switched from ectocochliate to endocochliate, and then back to ectocochliate late in embryogenesis. According to this model, the outer mantle reflexed back onto the outside of the ammonitella during the endocochliate stage, secreting the outer prismatic layer and tuberculate micro-ornamentation.

The micro-ornamentation on the postembryonic shells of these ceratites consists of ridges and tubercles aligned in longitudinal rows. In some specimens, the ridges and tubercles follow a concave pattern on the inner flanks and a straight, prorsiradiate pattern on the outer flanks. This ornamentation occurs on a thin prismatic layer on both the venter and flanks.

Our data suggest that there is an ontogenetic change in the appearance of this micro-ornamentation. In early postembryonic growth, the micro-ornamentation consists of discontinuous, transverse lirae composed of interconnected tubercles (Fig. 6E, left arrow). During ontogeny, the network of tubercles becomes more distinct, and the tubercles themselves become more ridge-like (Fig. 8A, D, F). In still later ontogeny, it is possible that these ridges unite to form longitudinal striae.

A similar micro-ornamentation has been documented in three genera of Jurassic ammonites including *Quenstedtoceras* (see Kulicki, 1974, pl. 4, figs. 1, 2), *Kosmoceras* (see Kulicki, 1979, pl. 48, fig. 4; Sprey, in press, fig. 1), and *Binatisphinctes* (see Sprey, in press, figs. 2, 3B). The micro-ornamentation consists of tubercles and ridges aligned in longitudinal and transverse rows in *Quenstedtoceras* and *Kosmoceras* and in longitudinal and prorsiradiate rows in *Binatisphinctes*. In all three genera, the ridges and tubercles occur on a thin prismatic layer marked by occasional growth lines.

This micro-ornamentation is reminiscent of the tuberculate micro-ornamentation on the ammonitella but there are many differences. The tubercles on the postembryonic shell are larger and more asymmetric than those on the ammonitella. The tubercles on the postembryonic shell are also aligned in longitudinal rows, whereas they are irregularly distributed on the ammonitella. In addition, growth lines or growth discontinuities are present on the surface of the postembryonic shell, whereas they are absent on the ammonitella.

The micro-ornamentation on these postembryonic shells resembles the wrinkle layer, which is secreted as part of the dorsal wall (Walliser, 1970; House, 1971; Senior, 1971; Tozer, 1972; Kulicki, 1979; Kulicki *et al.*, in press, a). This layer generally covers the surface of the preceding whorl and extends some distance adoral of the aperture. It forms a wide variety of patterns (Walliser, 1970, fig. 3), although none of these patterns exactly matches the micro-ornamentation described here. Nevertheless, the asymmetric profile of many of the tubercles on these ceratites, with a gently sloping adapical face and a more steeply sloping adoral face, is characteristic of the elements of the wrinkle layer (Kulicki, 1979, fig. 9).

Tozer (1972, p. 642) noted spiral ornamentation in the Triassic ceratite *Discotropites* and cited a specimen of *Discotropites laurae* (Mojsisovics, 1893) illustrated by Smith (1927, pl. 11, fig. 8) that displayed this feature. A similar ornamentation also occurs in *Amaltheus* (see Zittel, 1924, p. 575, fig. 1218; Walliser, 1970, pl. 4, fig. 5). However, unlike the micro-ornamentation described here, the ornamentation in both of these genera consists of only spiral ridges, not tubercles, and Tozer (1972, p. 643) considered both of them to have been secreted as part of the dorsal wall.

Despite the superficial resemblance to the wrinkle layer, the micro-ornamentation on the postembryonic shells of our ceratites probably did not form as part of the dorsal wall. If the micro-ornamentation had been secreted by a supracephalic mantle fold, this ornamentation would have covered the boundary between the ammonitella and postembryonic shell. Instead, the micro-ornamentation appears abruptly at the start of the postembryonic shell.

It is more likely that the postembryonic micro-ornamentation formed at the apertural margin. The tubercles were probably secreted at specific sites along the mantle edge. As the shell grew, the tubercles formed a series of longitudinal rows. The micro-ornamentation on the shell probably reflected that of the periostracum. A similar phenomenon has been observed in modern *Nautilus* in which spherical bundles of crystals form at the growing edge of the mantle at the intersection of spiral and radial lirae (see Arnold *et al.*, 1987, fig. 7). These lirae reflect the ornamentation of the periostracum.

FUTURE WORK

It is important to examine members of other ceratite families to determine if they also display a tuberculate micro-ornamentation on the ammonitella. Previous studies (Landman *et al.*, 1996) have suggested that the kind of micro-ornamentation on the ammonitella is invariant at the subordinal level. However, additional sampling is recommended. Along the same lines, we need to examine members of other suborders in which the micro-ornamentation on the ammonitella is still unknown. The most notable omission is the Prolecanitina, which is presumed to be ancestral to the Mesozoic ammonoids (House, 1988, Text Fig. 4). Lastly, we need to evaluate the variation in tuberculate micro-ornamentation among Mesozoic suborders to develop a set of character states useful for investigating relationships within this group. Such character states may include the size, microstructure, and distribution of tubercles on the shell surface.

The mode of formation of the micro-ornamentation on the postembryonic shell is puzzling. To resolve this issue, it is important to document other occurrences of this micro-ornamentation. Does this micro-ornamentation occur at the apertural margin in specimens with preserved apertures? Does a dorsal shell layer also cover the preceding whorl? The presence of the same micro-ornamentation in three genera of Jurassic Ammonitina and one genus of Triassic Ceratitina suggests that it is widespread. Does it occur in still other genera?

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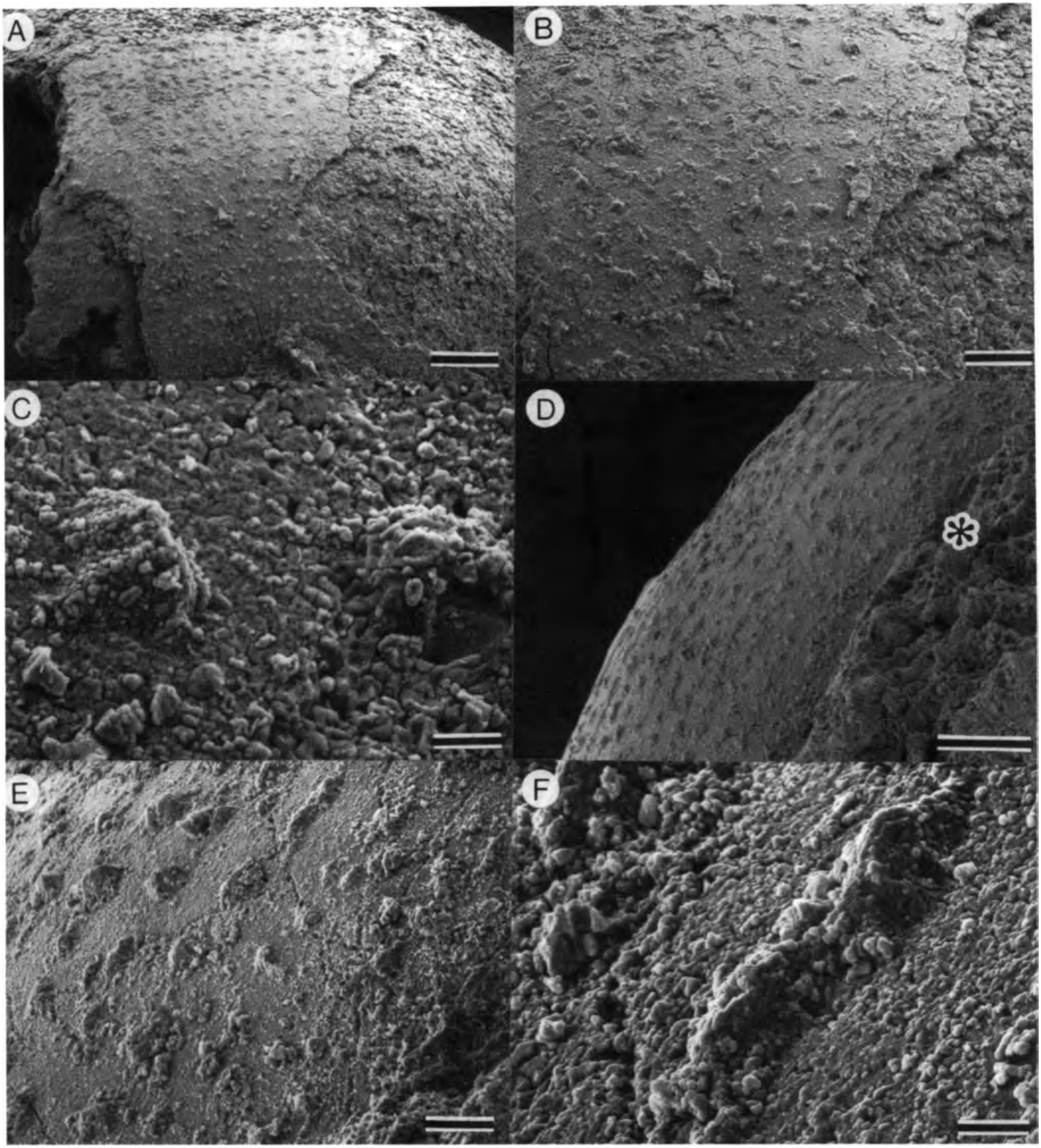

Fig. 8. *Trachyceras (Trachyceras) muensteri* (Wissmann, 1841), AMNH 46599, San Cassiano Formation, Dolomites, Italy. A. The micro-ornamentation is visible on the early postembryonic shell. The adoral direction is toward the right. Scale bar = 60 µm. B. The tubercles are aligned in longitudinal rows. The adoral direction is toward the right. Scale bar = 30 µm. C. The tubercle on the left has an asymmetric profile with a gently sloping adapical face and a more steeply sloping adoral face. The adoral direction is toward the right. Scale bar = 3 µm. D. Overview of the same specimen one-third whorl adoral of A. The adoral direction is toward the upper right. The asterisk indicates the position of E. Scale bar = 60 µm. E. No growth lines are visible on the surface of the shell. Scale bar = 15 µm. F. Close-up of a ridge elongated in the longitudinal direction. Scale bar = 3 µm.

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