JOURNAL OF PALEONTOLOGY, V. 56, NO. 2, P. 386–391, 2 TEXT-FIGS., MARCH 1982

MICRO-ORNAMENT ON EARLY WHORLS OF MESOZOIC AMMONITES: IMPLICATIONS FOR EARLY ONTOGENY

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ABSTRACT—Tuberculate micro-ornamentation occurs on the exposed embryonic whorls of the shells of some Jurassic and Cretaceous ammonites and extends to the nepionic constriction. This plus the absence of growth lines on the embryonic shell argue against the existence of a larval form in early ammonite ontogeny. Like modern cephalopods, ammonites apparently had direct development.

INTRODUCTION

SCANNING electron (SEM) observations of the external ornament on the earliest whorls of certain well-preserved ammonites (see Table 1) reveal a consistent distribution of tuberculate sculpture not readily apparent either at conventional magnifications or in SEM studies of ammonites in thin section. In independent observations Bandel found this feature in *Baculites, Quenstedtoceras* and *Kosmoceras* and Landman and Waage found it in several genera of scaphitids and *Sphenodiscus*.

Our use of two terms common in ammonite ontogeny deserves clarification. The term *embryonic shell* includes the shell of the protoconch and early whorls up to and slightly beyond the nepionic constriction. This is the *ammonitella* of Drushits and Khiami (1970, p. 27–30), a term which we will use interchangeably with embryonic shell. The term *nepionic constriction* itself refers here to the shallow groove on the external shell produced by a constriction in the aperture of the shell at that point. It is a primary feature that corresponds approximately but not precisely in position to the similar groove formed on steinkerns by the local internal thickening of the shell referred to by some authors as the *primary varix* (Drushits and Khiami, 1970, p. 27–30; Grandjean, 1910, p. 512) or *second growth change* (Erben, 1964, p. 161–164; Erben, Flajs and Siehl, 1969, p. 26). Apparently, there is some misunderstanding about the existence of an actual constriction in the shell itself at this location. Drushits and Khiami (1970, p. 27) in recommending the term primary varix in place of nepionic constriction state "the reality consists of an abrupt thickening of the shelly layer in the conch wall, whereas the constriction develops only after the ammonite's burial and the formation of a natural cast." An external nepionic constriction exists on the embryonic shell of all the ammonites here studied (see Table 1); examples in Text-fig. 1C and 2A show this clearly.

Bandel first observed the tuberculate external ornament of embryonic shells on silicified ammonitellas of *Baculites*. These were extracted using acetic acid from limestone adjacent to chert found in highly fossiliferous silicified and phosphatized Upper Cretaceous (Campanian and Maastrichtian) formations in northern Jordan. Subsequently similar tuberculate structure was found on embryonic shells of *Quenstedtoceras* and *Kosmoceras* from erratic boulders in the glacial deposits of Lukow, Poland. Also exceptionally well preserved and essentially unaltered, this material can be prepared much like modern shell material and its structure and composition studied in detail.

Landman first noted the tubercular external ornament on the embryonic shells of three genera of scaphitids in his ontogenetic study of Turonian to Santonian scaphitid genera in the Western Interior of the United States. Similar ornament was subsequently found by Waage in Maastrichtian scaphitids and *Sphenodiscus,* both from the same region. Recovery of early whorls from the well-preserved material from these stratigraphic levels was done by simple dissection of specimens.

Micro-ornamentation on the embryonic whorls has been observed before on some Jurassic and Upper Cretaceous ammonites. James Perrin Smith (1901, p. 42) recognized the fine tuberculate ornamentation on the early coil of *Baculites chicoensis* from the Upper Cretaceous of California, noting that the "pustules" gave the shell a granulated appearance and did not extend beyond the nepionic constric-

0022-3360/82/0056-0386$03.00

TABLE *1*—Ammonite species studied.

Ammonites species	Age (formation)	Locality
Scaphites whitfieldi Cobban	Turonian (Carlile Shale)	South Dakota
Scaphites preventricosus Cobban	Coniacian (Marias River Shale)	Montana
Clioscaphites vermiformis (Meek and Hayden)	Santonian (Marias River Shale)	Montana
Pteroscaphites auriculatus (Cobban)	Coniacian (Marias River Shale)	Montana
Discoscaphites conradi (Morton)	Maastrichtian (Fox Hills Formation)	South Dakota
Hoploscaphites nicoletti (Owen)	Maastrichtian (Fox Hills Formation)	South Dakota
Hoploscaphites sp. juveniles	Maastrichtian (Fox Hills Formation)	South Dakota
Sphenodiscus lenticularis (Owen)	Maastrichtian (Fox Hills Formation)	South Dakota
Baculites chicoensis Trask	Campanian	California
Baculites sp.	Campanian, Maastrichtian	North Jordan
Quenstedtoceras sp.	Callovian	Lukow, Poland*
Kosmoceras sp.	Callovian	Lukow, Poland*

* Erratic boulders.

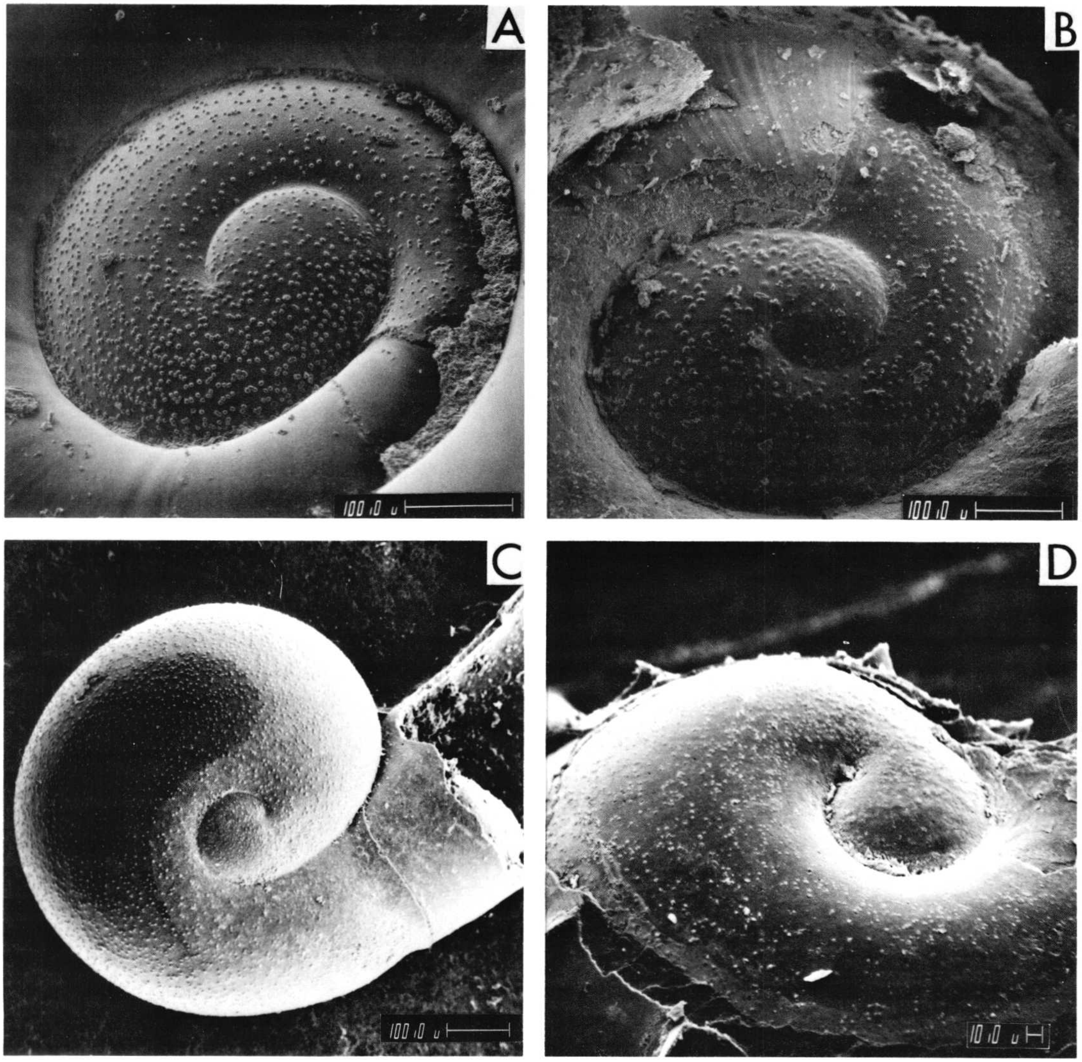
tion. Even earlier, Brown (1892, p. 139) recorded the presence of "minute tuberculations of irregular shape" on the embryonic shell surface of *Baculites compressus.* W.D. Smith (1905, p. 642) studying *Scaphites nodosus* from the Western Interior of North America noted "regular rows of small pustules . . . ceasing abruptly at a constriction" on embryonic shells of this species. More recently, Kulicki (1974, p. 206–209) described the small tubercles on the ammonitellas of *Quenstedtoceras* and *Kosmoceras,* and noted their continuity across the entire ammonitella to, but not beyond, the nepionic constriction. Subsequently (1979, p. 117, pl. 38, figs. 1a, b, pl. 48, fig. 3), he observed the presence of "small tubercles" in thin sections of the wall of the embryonic shell of *Quenstedtoceras* and illustrated the tuberculate ornament on an SEM photo of a fragment of the embryonic shell of *Kosmoceras*.

DESCRIPTION

On all ammonites observed by the authors (see Table 1) the fine tubercles are irregularly distributed over and restricted to the exposed portions of the ammonitella (Text-fig. 1, A–D). The tubercles may die out at the adapical edge of the nepionic constriction, within its shallow depression, or on the narrow extension of the embryonic shell adoral to the constriction. They have not been observed beyond the abrupt termination of the embryonic shell. The new, outer prismatic shell layer that emerges from beneath the embryonic prismatic shell at this point is non-tuberculate and its smooth surface is commonly marked by very fine transverse ridges that probably represent growth lines (Text-figs. 1B, 2A). The tuberculate embryonic shell is devoid of growth lines or other linear ornament of any kind in all specimens we have observed.

The tubercles of the embryonic shell of all ammonites studied seem to be scattered without apparent pattern and small open patches of shell surface without any tubercles occur. The structure of the embryonic outer shell wall seen in section is spherulitic-prismatic and the tubercles appear to be largely spherulitic in structure, consisting of bundles of needle-like crystals radiating outward from points within the wall, i.e., like sectors of spherules. From an external view single larger tubercles clearly show terminations of a number of prisms (Text-fig. 2C). In some of the scaphitid specimens from North America, which may not be quite as well preserved as the Lukow material, some smaller tubercles appear to be the emergent ends of single large prisms but the larger ones show the more complex spherulitic structure (Text-fig. 2B). Kulicki (1979, p. 117) noted in thin sections of the embryonic shell of *Quenstedtoceras* small tubercles formed by extensions of prisms and sometimes characterized by a spherulitic structure. Probably the tubercles were all originally spherulitic but in some recrystallization has obliterated the structural detail.

The observed tubercles range from about 2 to almost 10 μm in diameter. Within one individual as well as in individuals of the same species they are somewhat variable in size, the largest being those with obvious spherulitic structure. *Sphenodiscus* and *Quenstedtoceras* have very small tubercles, approximately 2–3 μm in diameter. The tubercles of scaphitids and *Baculites* are similar in size with diameters mostly in the 4–8 μm range. In one *Scaphites whitfieldi* specimen in which it was pos-

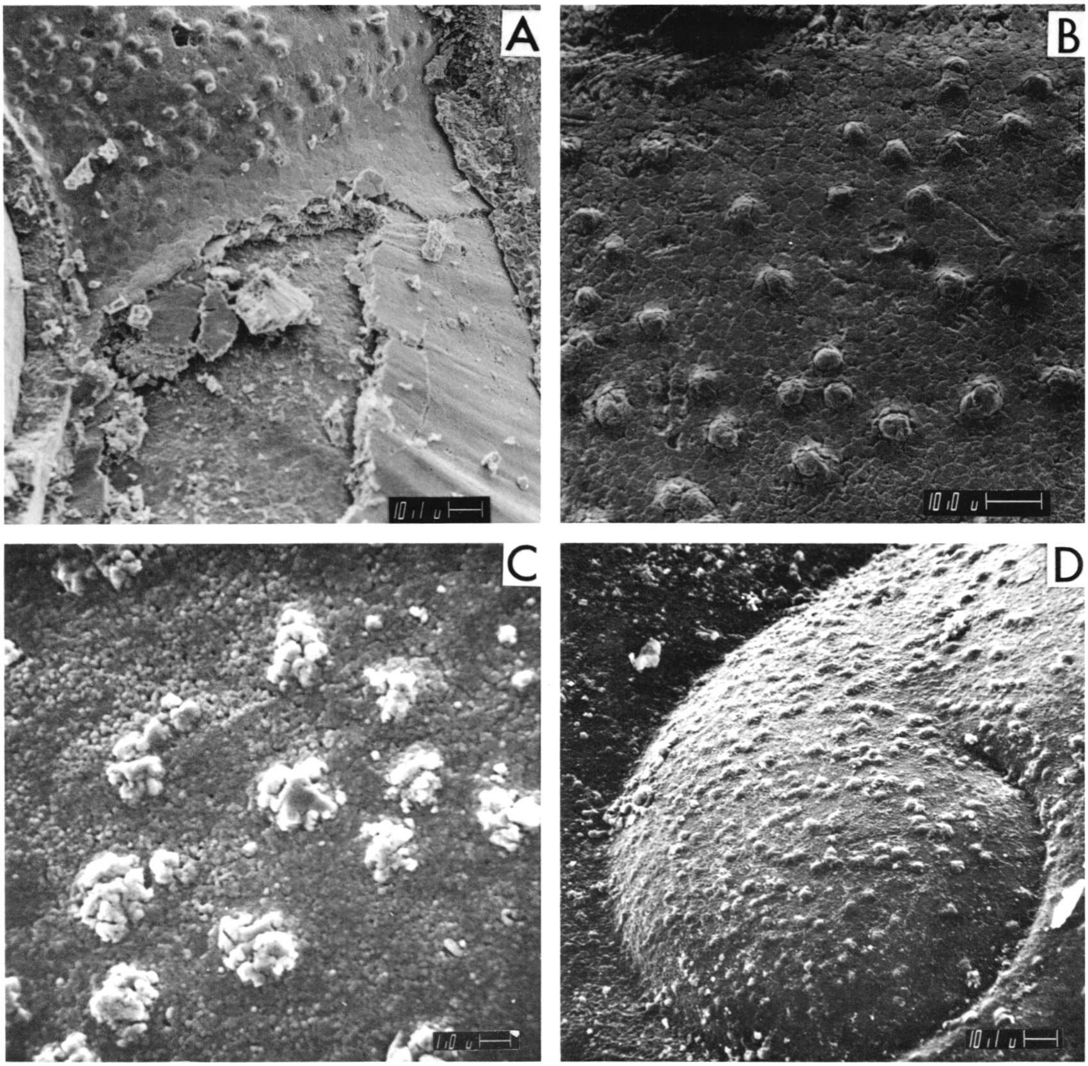


TEXT-FIG. *1*—Micro-ornament on external embryonic shells of ammonites. *A, Hoploscaphites* sp., juvenile, edge of embryonic shell is broken at nepionic constriction. *B, Clioscaphites vermiformis,* apparent "color" change occurs at nepionic constriction. *C, Baculites* sp., note abrupt edge of embryonic shell adoral of nepionic constriction. *D, Quenstedtoceras* sp.

sible to measure the height of tubercles in section they were approximately 2 μm high.

DISCUSSION

The external features of the embryonic shell of ammonites are known from too few genera to draw any general conclusions about the distribution of tuberculate micro-ornament among the Ammonoidea as a whole. At least one other kind of external embryonic sculpture has been described. House (1965, p. 87) has shown that in the Devonian goniatite *Tornoceras,* "The protoconch and first whorl are ornamented by convex evenly spaced raised lirae" which disappear at the nepionic constriction and, beyond it, are replaced by a different sculpture (growth lines?) of "biconvex lirae which show a prominent ventrolateral salient and a deeper, narrower, ventral sinus." The cessation of the embryonic sculpture at the nepionic constriction, as in the ammonites with tuberculate micro-ornament, suggests that



TEXT-FIG. 2—*A, Clioscaphites vermiformis,* close-up of nepionic constriction; tuberculate micro-ornamentation ends and growth lines begin; postembryonic shell emerges from beneath embryonic shell. *B, Hoploscaphites* sp., juvenile, close-up of tubercles. *C, Quenstedtoceras* sp., close-up of tubercles. *D, Baculites* sp., close-up of tubercles.

Tornoceras also had a similar ontogenetic development.

Drushits, Doguzhayeva and Mikhaylova (1977, p. 197) in reference to ammonites in general state that "the surface of the protoconch and the first whorl is smooth as far as the nepionic line, without any trace of sculpture"; and Drushits and Khiami (1970, p. 27) make a similar statement in regard to Cretaceous ammonites. Both of these important studies of ammonite development utilized SEM observations of sectioned specimens. Tuberculate micro-ornament is difficult to observe in thin sections and polished cross sections of ammonites because of the relatively small size and scattered distribution of the tubercles. It is also possible that these authors in referring to sculpture meant only the more pronounced and regular sculptural patterns of the postembryonic shell. There may indeed be smooth embryonic shells in some groups of ammonites, but it is not sufficient to assume this from SEM inspection of sections alone; direct observation of the exterior of the embryonic shell is essential. The fact that the nine genera in this study, all observed to have tuberculate micro-ornament, represent four different ammonite superfamilies suggests that this feature is widespread.

A model for the mineralization of the embryonic shell which explains the absence of growth lines is proposed by Bandel (in press). An analogy is made with some modern archaeogastropods in which initially an organic embryonic shell is produced. Soon after, the organic shell is rapidly mineralized by prismatic needles of aragonite which grow into and replace it. This forms a shell which has no growth lines and consists of a first mineral layer of uniform thickness that preserves the original ornamentation of the organic shell (Bandel, 1979, p. 50–52). Similarly, Bandel proposes that in ammonites an originally organic embryonic shell was mineralized simultaneously. This formed a spherulitic-prismatic layer of uniform thickness on all exposed portions of the ammonitella. All other mineral layers were deposited subsequent to this first mineralization. By contrast, molluscs which form their embryonic shell by secreting mineralized shell increments from the beginning usually show growth lines on their embryonic shells (Bandel, 1975).

Bandel's model of early ammonite ontogeny differs from that of Erben (1964, 1966) and Erben, Flajs and Siehl (1969) based on analogy with the higher prosobranch gastropods. In these gastropods as well as in pulmonates and in neritaceans and opisthobranchs with a free living marine larval stage, the larval shell is characterized by the presence of growth lines. Usually the embryonic shell differs in sculpture from the larval shell and the larval shell differs in sculpture from the adult shell. Growth lines also occur in recent bivalves and scaphopods where their first appearance documents a drastic change in early ontogeny such as hatching or metamorphosis.

In summary, the restriction of the tuberculate external sculpture to the ammonitella, the absence of growth lines, the external uniformity of the embryonic shell and absence of any surface indication of internal structural changes, and the striking contrast between the ammonitella and the shell surface beyond the nepionic constriction, suggest deposition in a uniform physico-chemical environment different from that of the postembryonic shell. This conforms with Bandel's model and supports the position of Drushits and Khiami (1970), Drushits, Doguzhayeva and Mikhaylova (1977), Kulicki (1974, 1979) and Birkelund and Hansen (1974) that the nepionic constriction marks the position on the shell when the ammonite animal hatched from its egg capsule. There certainly appears to be no external evidence of an intervening larval stage after formation of the protoconch as postulated by Erben (1964, 1966) and Erben, Flajs and Siehl (1969). That ammonites did not have a distinct larval form but rather direct development is in keeping with all modern cephalopods whose development is known (Arnold and Williams-Arnold, 1977, p. 282; Wells and Wells, 1977, p. 329–330; Bandel and Boletzky, 1979, p. 324–335).

ACKNOWLEDGMENTS

We thank Jost Wiedmann of Tubingen who noticed our separate studies and suggested joint publication. G. Dietl of the Naturkundemuseum in Stuttgart kindly made available the exceptional material from the Lukow boulders. We thank Tove Birkelund, William A. Cobban, Peter Ward and Gerd Westermann for reviewing the manuscript. Alan Pooley, Yale Peabody Museum, did the SEM work and William Sacco the photographic reproductions for Landman and Waage; these were supported by NSF Grant DEB78-12518 and the Schuchert Fund of Yale Peabody Museum.

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MANUSCRIPT RECEIVED MARCH 2, 1981
REVISED MANUSCRIPT RECEIVED AUGUST 3, 1981