

Early Life History of Carboniferous Ammonoids Inferred from Analysis of Shell Hydrostatics and Fossil Assemblages

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This paper discusses postembryonic early mode of life in Carboniferous goniatites based on analysis of ammonoid assemblages and calculation of total shell densities of actual specimens. Co-occurrence of embryonic and postembryonic shells appears common in Carboniferous Goniatitina, as confirmed in Homoceras, Homoceratoides, Vallites, and Reticuloceras from the Middle Carboniferous (Namurian) of west Ireland and England, in Tumulites, Cravenoceras and Eumorphoceras from the Upper Mississippian (Chesteran) of Texas, and in Aristoceras and Vidrioceras from the Upper Pennsylvanian (Virgilian) of Kansas. Embryonic and postembryonic shells of these genera occur in ammonoid-packed calcium carbonate concretions (bullions) or in black bituminous limestone beds, together with rare shells of bactritoid cephalopods, brachiopods, bivalves and gastropods. They appear to not have been transported a long distance be-

cause of the absence of a preferred orientation, size sorting and apparent shell abrasion or fragmentation. Buoyancy calculation of specimens of 12 species belonging to 8 genera including Homoceras, Aristoceras, and Vidrioceras from several fossil localities shows that the total shell densities at hatching remain almost constant among these species and can be approximated to that of seawater (=neutral buoyancy). These lines of evidence strongly suggest a similarity in the biostratinomic properties of empty shells between post-hatching juvenile stage and middle-late ontogeny. In all probability, in most Carboniferous Goniatitina, a newly hatched ammonoid had a nektobenthic or nektic mode of life, as has been postulated for adult animals.

INTRODUCTION

The embryonic ammonoid shell, or ammonitella, consists of a spherical initial chamber (protoconch) and subsequent planispiral whorl with a thickening of the nacreous shell layer (primary varix) at the aperture. The boundary between the ammonitella and post-ammonitella stages is marked by the appearance of a conspicuous constriction (primary constriction) from which the shell structure, surface ornament and whorl growth change synchronously. Most recent workers regard the ammonitella as the embryonic shell that formed within an egg capsule, and that ammonoids hatched immediately after the formation of the primary constriction (Birkelund and Hansen,

1968; Drushits and Khiami, 1970; Kulicki, 1974, 1979; Drushits et al., 1977; Tanabe et al., 1980; Bandel, 1982, 1986; Landman, 1982; Tanabe, 1989; Landman et al., in press). This interpretation is strongly supported by the presence of a similar constriction in newly hatched *Nautilus* shells (Okubo, 1989; Carlson, 1991).

Minute ammonoids referable to embryonic and/or early postembryonic shells have been known from several Jurassic and Cretaceous genera such as *Arnioceras* (Trueman, 1941), *Harpoceras* (Wetzel, 1959), *Quenstedtoceras* (Kulicki, 1974, 1979; Blind, 1979), *Baculites* (Landman, 1982), and *Scaphites* (Landman, 1985), but their occurrence in the marine Mesozoic is generally rare and sporadic as compared with that of medium- to large-sized ammonoids.

While investigating paleobiological aspects of Paleozoic ammonoids based on samples from various regions throughout the world, we have noticed that co-occurrence of embryonic and postembryonic ammonoids is fairly common in ammonoid-packed carbonate concretions, or bullions, in Carboniferous deposits. Based on the analysis of such assemblages from northwestern Europe and the mid-continent of the United States and calculation of total shell densities of actual specimens, we discuss the postembryonic early life history in Carboniferous Goniatitina.

All specimens utilized are deposited at the University Museum of the University of Tokyo (UMUT).

SHELL HYDROSTATICS

Material and Methods

A total of 32 immature postembryonic specimens of 12 species belonging to 8 genera listed in Table 1 were used for buoyancy calculations. Each specimen was cut and polished along the median plane, and then the half specimen was further cut vertically at the base of the caecum. The initial chamber of each specimen was divided into three parts, 0–1.0 π , 1.0–1.5 π , and 1.5–2.0 π in rotation angle, and the volume in each part was approximated as a part of an ellipsoid (see

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TABLE 1—Hydrostatic properties of 12 Carboniferous goniatite species at hatching. IC: initial chamber diameter, AD: ammonitella diameter, VI: initial chamber volume, AV: ammonitella volume, AW: ammonitella weight. Mean value of *H. subglobosum* is used for calculation of the mean of the 12 species.

Species	Speci- men (UMUT PM)	IC (mm)	AD (mm)	VI (cm ³)	AV (cm ³)	VI/AV	AW (mg)	Total den- sity	Locality and horizon
<i>Homoceras subglobosum</i> (Bisat)	19331-1	0.512	0.936	0.075	0.370	0.203	0.364	0.984	Stonehead Beck, England (Namurian)
	-2	0.471	0.899	0.062	0.339	0.183	0.340	1.003	
	-3	0.466	0.911	0.058	0.303	0.191	0.302	0.997	
	-4	0.513	0.977	0.070	0.350	0.200	0.345	0.986	
	-5	0.467	0.885	0.050	0.268	0.187	0.268	1.000	
	-6	0.517	0.950	0.070	0.388	0.180	0.390	1.005	
	-7	0.520	0.981	0.065	0.350	0.184	0.350	1.000	
	-8	0.504	0.913	0.058	0.287	0.202	0.282	0.983	
	-9	0.470	0.887	0.056	0.280	0.200	0.276	0.986	
	-10	0.431	0.891	0.044	0.249	0.177	0.251	1.008	
	-11	0.487	0.922	0.062	0.298	0.210	0.291	0.977	
	-12	0.477	0.937	0.061	0.333	0.183	0.333	1.003	
	-13	0.478	0.922	0.059	0.325	0.182	0.326	1.003	
	-14	0.506	0.956	0.061	0.325	0.188	0.324	0.997	
	-15	0.450	0.846	0.054	0.327	0.165	0.334	1.021	
	-16	0.484	0.860	0.059	0.290	0.203	0.285	0.983	
	-17	0.471	0.925	0.060	0.311	0.193	0.309	0.994	
	-18	0.488	0.899	0.057	0.270	0.211	0.264	0.978	
	-19	0.510	0.927	0.063	0.288	0.328	0.278	0.965	
	-20	0.466	0.859	0.059	0.290	0.203	0.284	0.979	
	-21	0.510	0.938	0.064	0.302	0.212	0.294	0.974	
Mean		0.486	0.915	0.060	0.312	0.199	0.309	0.992	
Standard dev.		0.024	0.036	0.007	0.035	0.031	0.036	0.013	
<i>Goniatites aff. crenestria</i> Phillips	19332	0.474	0.964	0.059	0.330	0.179	0.332	1.006	Ahloso, Oklahoma (Chesteran)
<i>Goniatites multiliratus</i> Gordon	19333	0.534	0.939	0.067	0.375	0.179	0.384	1.024	Jack Fork Creek, OK (Chesteran)
<i>Goniatites choctawensis</i> Shumard	19334	0.544	1.030	0.094	0.468	0.201	0.461	0.985	Clarita, OK (Chesteran)
<i>Glaphyrtes hyattianus</i> (Girty)	19335	0.507	1.005	0.074	0.430	0.172	0.436	1.014	Okmulgee, OK (Desmoinesian)
<i>Glaphyrtes clinei</i> (Miller & Owen)	19336	0.462	0.874	0.047	0.239	0.197	0.236	0.987	Collinsville, OK (Desmoinesian)
<i>Glaphyrtes warei</i> (Miller & Owen)	19337	0.481	0.900	0.066	0.358	0.184	0.358	1.000	Collinsville, OK (Desmoinesian)
<i>Gatherites</i> sp.	19338	0.456	0.891	0.057	0.283	0.201	0.278	0.982	Okmulgee, OK (Desmoinesian)
<i>Bisatoceras</i> sp.	19339	0.344	0.643	0.023	0.120	0.192	0.119	0.992	Okmulgee, OK (Desmoinesian)
<i>Eothallassoceras inexpectans</i> (Miller & Owen)	19340	0.321	0.639	0.017	0.086	0.198	0.085	0.988	Okmulgee, OK (Desmoinesian)
<i>Aristoceras</i> sp.	19341	0.340	0.665	0.022	0.123	0.179	0.124	1.008	Pomona, Kansas (Virgilian)
<i>Vidrioceras</i> sp.	19342	0.473	0.901	0.049	0.258	0.190	0.257	0.996	Pomona, Kansas (Virgilian)
Mean of 12 species		0.452	0.864	0.053	0.278	0.189	0.282	0.996	
Standard dev.		0.072	0.132	0.022	0.118	0.010	0.118	0.010	

Shigeta, 1993 for details). The volume of the initial chamber is thus expressed as a sum of the volume of the three parts. Three radii of each part were measured by means of a

digital micrometer (accuracy $\pm 1 \mu\text{m}$) attached to a NIKON V16 profile projector.

Concerning the whorls, the increasing rate of their volume (dV) is

expressed by the following formula (Shigeta, 1993).

$$dV = SR d\theta,$$

where S is the area of whorl cross

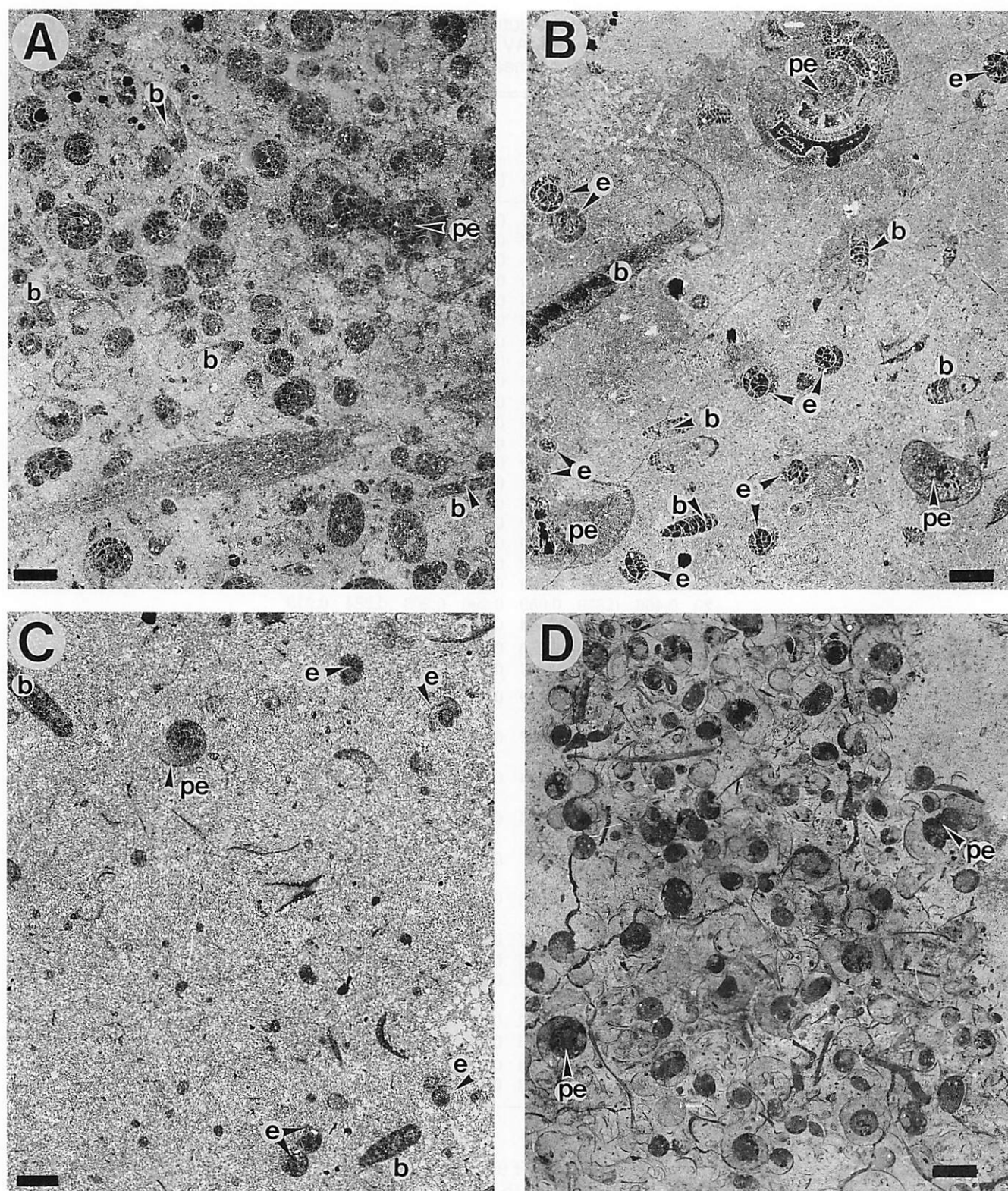


FIGURE 1—Photomicrographs of the embryonic ammonoid-bearing slabs in thin section. All scale bars represent 1 mm. pe: postembryonic ammonoids, b: embryonic bacritoids. A) Densely packed embryonic ammonoids referred to *Reticuloceras*, *Vallites*, and *Homoceratoides*, with

section, R is the radius vector from the center of coiling defined as a half point of whorl height, θ is the total rotation angle, and d is the increase of rotational angle. The relationship between S and R in many ammonoids may be expressed by the following equation (Trueman, 1941).

$$SR = b \exp^{a\theta},$$

where a is defined as the volume expansion rate and b is a constant. Using these relationships, the volume of a given half whorl may be expressed as:

$$V = \int_0^x b \exp^{a\theta} d\theta \quad (0 < x < 1\pi)$$

The volume of the shell material was estimated to be 8% of the volume of the body whorl, since the shell thickness at a given point in the ammonitella is about 2% of the whorl height in many specimens examined. The prosepium was not taken into account in the volumetry of the shell material. The densities of shell material and soft tissues were regarded as 2.62 g/cm³ and 1.055 g/cm³ respectively, in accordance to the data on living *Nautilus* (Saunders and Shapiro, 1986). Following the microscopic observations (see Appendix), we calculated the total shell density of each specimen at hatching on the assumption that an early postembryonic goniatite had a shell consisting of a gas-filled initial chamber (protoconch) and a subsequent body chamber terminated at the primary constriction.

We did not calculate the total shell densities of the 12 species in the postembryonic stage, because exact data on the volumes of the shell wall, septa, siphuncle, cameral liquid, and body chamber length at different

growth-stages were not available in the specimens studied.

Results

Disregarding cameral liquid, the total shell densities at hatching in the 12 species of the Goniatitina are fairly similar to one another and range from 0.982 to 1.024 with an average of 0.996 (Table 1). These densities are slightly less than the density of sea water (=1.026). However, if some amounts of cameral liquid are included within the initial chamber, the total densities may approximate to that of sea water in most species. Indeed, the presence of a small amount of cameral liquid has been confirmed in embryos and newly hatched animals of Recent *Nautilus* by radiographic examinations (K. Tanabe's unpublished data).

DISCUSSION

As a result of hydrostatic examinations, it was realized that the specimens of the 12 Carboniferous goniatite species have almost constant total shell densities at hatching which are almost equivalent to the density of sea water. Meanwhile, calculation and computer-based simulation of shell hydrostatics by Saunders and Shapiro (1986) and Swan and Saunders (1987) have shown a neutral buoyancy condition in many Carboniferous ammonoids in the postembryonic stage, since the buoyancy, stability, and orientation are closely linked with morphometric variables such as shell geometry, body chamber length, and shell thickness in many species. These lines of evidence seem to suggest that the 12 species examined kept a neutrally buoyant condition not only at the hatching stage but also during

postembryonic growth. Under such circumstances, it is expected that empty ammonoid shells of various growth-stages including embryonic shells would have accumulated in the same places as a reflection of their uniform hydraulic behavior during biostratinomic processes. The frequent co-occurrence of embryonic and postembryonic ammonoids in the Carboniferous deposits described by Ramsbottom (1977, 1980) and ourselves (see Appendix) is consistent with the above prediction. In all probability, most Carboniferous Goniatitina had a constant, possibly nektic or nektobenthic mode of life in relatively offshore, low-energy habitats, without a postembryonic planktic stage.

In contrast to the situation in Carboniferous Goniatitina, the occurrence of embryonic and early postembryonic shells in the Mesozoic strata is quite episodic and peculiar. They occur profusely in fine-grained sediments (carbonate concretions, micritic limestones, mudstones) of Jurassic to Cretaceous age, commonly showing sheltered preservation within the body chambers and adhering matrix of larger ammonites (Trueman, 1941; Wetzel, 1959; Drushits and Khiami, 1970; Kulicki, 1979; Birkelund, 1979; Kulicki and Wierzbowski, 1983; Landman, 1985). Embryonic and early postembryonic ammonoids hitherto described are frequently broken and are intermixed with small gastropods, bivalves, foraminifers, and fish scales. Landman (1985) suggested that these peculiar fossil assemblages may represent a mixed thanatocoenosis composed of organic remains of a variety of habitats.

Based on the above-mentioned peculiar appearance of embryonic and

fewer shells of postembryonic ammonoids and embryonic bacritoids. Middle Namurian bullion from Lisdoonvarna, west Ireland. UMUT PM 19325. B) Loosely packed embryonic and postembryonic shells of *Homoceras subglobosum*, with fewer embryonic bacritoid shells. Middle Namurian limestone (horizontal section = plane view) from Stonehead Beck, England. UMUT PM 19326. C) Dispersed embryonic and early postembryonic ammonoids (possibly belonging to *Cravenoceras*, *Eumorphoceras*, and *Tumulites*) and an unidentified bacritoid. Partly phosphatized Upper Mississippian (middle Chesteran) carbonate concretion (horizontal section = plane view) from San Saba, Texas. UMUT PM 19327. D) Densely packed embryonic shells of *Aristoceras* and *Vidrioceras*, with fewer postembryonic shells of the two genera. Upper Pennsylvanian (Virgilian) carbonate concretion (horizontal section = plane view) from Pomona, Kansas. UMUT PM 19328.

early postembryonic shells, Wetzel (1959) postulated a bottom crawling benthic life style for a newly hatched ammonite. However, most recent authors have considered that the newly hatched ammonite maintained a planktic life with the aid of a gas-filled, relatively large initial chamber (Kulicki, 1974, 1979; Birkelund and Hansen, 1974; Drushits et al., 1977; Landman, 1982, 1985; Tanabe and Ohtsuka, 1985). To verify this hypothesis, Shigeta (1993) calculated the ontogenetic changes of total shell densities in specimens of 71 Cretaceous ammonoid species, utilizing the same methodology applied to the Goniaticina in this paper. As a result, he realized that in all species, the total densities at hatching are markedly smaller (0.84–1.00; positively buoyant) than that of sea water, and the densities gradually increase with growth, attaining neutral buoyancy at a shell diameter between 2.0 and 2.5 mm. Based on these data, he concluded that Cretaceous ammonoids had a planktic life at hatching and presumably changed their mode of life from planktic to nektonic or nektonobenthic at this critical point. Shigeta's (1993) data are correlated well with the field evidence for the mode of occurrence that in many ammonoid assemblages, newly hatched specimens are rarely associated with medium- to large-sized specimens.

Available data on the embryonic shell morphometrics also indicate that the lengths of whorls (ammonitella angle) in the Carboniferous Goniaticina (340–420° in 26 species) are mostly longer than those in the Mesozoic Ammonitida (260–370° in 126 species) (Landman et al., in press, figs. 8–9). This fact causes the marked differences in the volume ratios of the initial chamber versus whole embryonic shell [e.g., 0.189 for the sample mean in the 12 species examined (Table 1) vs. 0.235 for the sample mean in 71 Cretaceous species (Shigeta, 1993, fig. 4)] and results in distinct differences in total shell densities at hatching (Landman et al., in press, fig. 7).

In conclusion, this work indicates that embryonic and early postembryonic shells of Carboniferous Goni-

aticina occur regularly in concretionary masses that sometimes represent hatching/post-hatching concentrations, and that these embryonic forms were neutrally buoyant.

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APPENDIX

We here describe the co-occurrence of embryonic and postembryonic ammonoids from four Carboniferous localities; (1) middle Namurian (lower Kinderscoutin, R_{1a}) in Lisdoonvarna, NW County Clare, west Ireland, (2) lower Namurian (Chokierian) in Stonehead Beck (formerly called Gill Beck), Cowling, south of Skipton, England, (3) Upper Mississippian (middle Chesteran) in San Saba, north of the Llano Uplift, central Texas, and (4) Upper Pennsylvanian (Virgilian) in Pomona, northeast Kansas. The lithology and mode of ammonoid occurrence at each locality are summarized below.

(1) Lisdoonvarna, west Ireland.—Ammonoids from this locality were found in several pieces of black bituminous calcium carbonate bullions which were collected by W. Bruce Saunders and others in 1974 on the left bank of the River Gowlaun, north of St. Brendan's Bridge, near Lisdoonvarna (=locs. 28-31 of Hodson, 1954). The pieces of bullions contain medium- to large-sized specimens of *Reticuloceras compressum*, *Homoceratoides magistrorum*, and *Vallites henkei*. Together with a few bactritoid shells, shells of embryonic and early postembryonic ammonoids possibly belonging to the above three species are densely packed in the bullion (Fig. 1A). Frequency of occurrence of embryonic and early postembryonic ammonoids is much higher than that of medium to large-sized ones; about 100 and 5 individuals per 1 cm² in thin section respectively. Due to secondary recrystallization, most ammonoid shells from the locality are not well preserved, but we could not find any trace of biostratigraphic biases such as shell breakage and size sorting in the limited samples available.

(2) Stonehead Beck, England.—A thin (ca. 15 cm thick) black micritic limestone concretionary lens yielding numerous embryonic and postembryonic ammonoids is intercalated in the black bituminous shale exposed at a small creek-side exposure along Stonehead Beck. It is rich in black mud with virtually no traces of bioturbation. Both embryonic and postembryonic ammonoids occur throughout the limestone lens, together with rare shells of bactritoid cephalopods (Fig. 1B). They are especially abundant in the lower and upper parts of the lens, showing a loosely packed, layered fabric 1-2 cm thick. *Homoceras subglobosum* is the most dominant ammonoid species in the assemblage. The frequencies of occurrence of embryonic and postembryonic shells, as observed in the horizontal section, are about 8 and 4 per 1 cm² respectively. Most embryonic and early postembryonic ammonoids are well preserved without apparent shell abrasion or fragmentation.

According to Ramsbottom (1977, 1980) and Saunders et al. (1979), the northwestern European marine Namurian sequences re-

corded 11 major cycles of transgression and regression that reflected global eustatic changes in sea level. Each major cycle comprises several small cycles (mesothems) in which minute ammonoid assemblages called "spat" occur repeatedly (Ramsbottom, 1980, fig. 2; Saunders et al., 1979, cover photo). The minute ammonoid-bearing limestone lenses at Stonehead Beck and bullions at Lisdoonvarna apparently correspond to Ramsbottom's (1977, 1980) "spat"-bearing horizons. Thus, available data strongly suggest that embryonic and early postembryonic ammonoids occur episodically in the Namurian of western Europe.

(3) North of Llano Uplift, San Saba, central Texas.—Embryonic and postembryonic ammonoids were collected by one of us (R.H.M.) in several discontinuous limestone beds in the upper Chesteran black to dark gray shale of the Barnett Formation (Plummer and Scott, 1937; Turner, 1970) exposed in north of the Llano Uplift (=locality M29B of Mapes, 1979). The limestone beds form discontinuous "concretions," each of which is about 40 cm in diameter and 15 cm in maximum thickness and is composed of black to gray micrite recrystallized to microsparite which grades to tan on the weathered surface. The lower half of the bed contains medium- to large-sized ammonoids of *Cravenoceras* sp., *Eumorphoceras* sp. and *Tumultites varians* (R.H. Mapes, unpublished observation), bioclasts of bivalves and brachiopods, and numerous silt-sized phosphate grains. Shell breakage and fragmentation are common in the ammonoids from this unit, suggesting a storm-generated or bioturbated origin of the fossil assemblage. Most ammonoids in the lower unit have been partly replaced by phosphate, and insoluble residues yield an abundant and diverse microfauna including conodonts, ostracods, benthic foraminifers, and embryonic ammonoids and bactritoids. The upper part of the bed is, in contrast, made of fine-grained, laminated mud without any trace of strong current action or bioturbation. Embryonic and early postembryonic ammonoids are scattered in the upper unit, together with less numerous bactritoids (Fig. 1C).

(4) Pomona, northeast Kansas.—Embryonic and postembryonic shells of *Aristoceras* sp. and *Vidrioceras* sp. occur in several carbonate concretions in an Upper Pennsylvanian (Virgilian) dysoxic, relatively offshore shale (Heebner Shale, Oread Formation) exposed at a road-side outcrop near the community of Pomona (Mapes et al., 1992; Tanabe et al., 1993). The concretions consist of fine-grained, laminated black mud with virtually no traces of bioturbation. Embryonic and early postembryonic shells of the two species occur throughout the concretions, together with bactritoids, bivalves, gastropods, and brachiopods. They show neither a preferred orientation nor size-sorting on sectioned concretion surfaces. The embryonic ammonoids are especially abun-

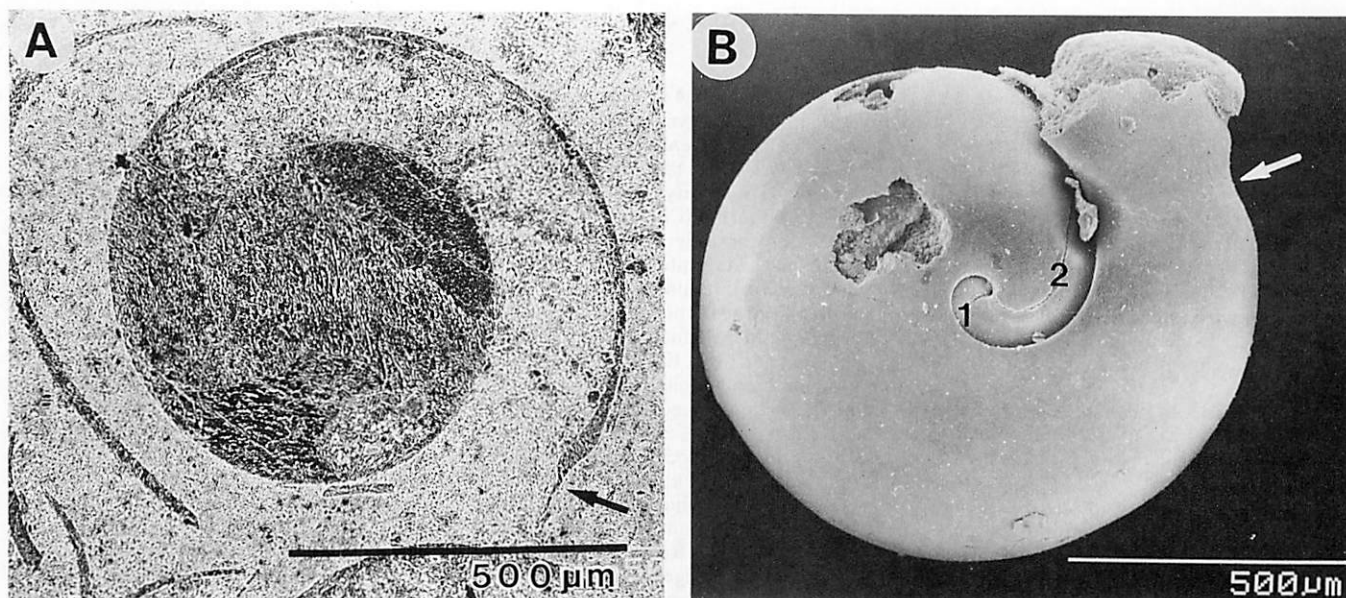


FIGURE 2—SEM micrographs of minute ammonoid shells. A) A fully grown embryonic shell of *Vidrioceras* just before hatching (median section). An arrow points to the primary varix at the aperture. UMUT PM 19329. From the Upper Pennsylvanian of Pomona, Kansas. B) An early postembryonic shell (steinkern) of *Cravenoceras* with two septa (1: proseptum, 2: second septum). An arrow points to the primary constriction. UMUT PM 19330. From the Upper Mississippian of San Saba, Texas.

dant and concentrated within a narrow interval in the middle part of the concretions, and form discrete lenticular concentrations. Within the concentrations the embryonic ammonoids are densely packed ($n = \text{ca. } 200/\text{cm}^3$) with fewer early postembryonic shells (Fig. 1D). Except for the tightly packed specimens in the middle part of the concretions, most embryonic and postembryonic ammonoids are well preserved without apparent shell abrasion and fragmentation. From these lines of evidence, Mapes et al. (1992) interpreted that the numerous well-preserved embryonic ammonoids in the con-

cretions were initially deposited on the bottom in egg masses at or in the immediate vicinity of the place where the concretions were formed at the fossil locality.

The ammonoid assemblages described above differ from one another in their age, lithology and mode of fossil occurrence. Optical and scanning electron microscopy of many specimens in thin section, however, reveals that the embryonic shells of each genus and/or species from these localities can be classified into three growth-stages; (1) early stage consisting of an incomplete initial chamber, (2) middle stage, consisting

of the initial chamber and part of the body chamber, and (3) late stage, consisting of the initial chamber and the complete body chamber with a primary varix at the aperture (=ammonitella) (see Tanabe et al., 1993, figs. 4–7). At every locality specimens at the late stage occur more abundantly than those at the early and middle stages. In fully grown embryonic shells (=ammonitellas), a pro-septum is present, but there are no septa nor is there a siphuncle (Fig. 2A). The septa and siphuncle were, therefore, undoubtedly formed in the postembryonic stage (Fig. 2B).

