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广东南雄晚白垩世恐龙蛋孵化期的微环境

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关键词　南雄盆地　晚白垩世　恐龙蛋　蛋窝微环境　气体传导率

内容提要

本文通过测量南雄盆地晚白垩世的三种恐龙蛋的蛋壳结构，估算了胚胎在正常发育的情况下蛋壳对水蒸汽和呼吸气体的传导率。结果发现，同现生鸟蛋的有关量相比，南雄恐龙蛋的气体传导率很高，蛋窝微环境具有湿度高、氧气含量低和二氧化碳含量高的特点。笔者推测这三种恐龙蛋是埋藏孵化的。从蛋壳结构来看，导致高气体传导率的直接因素是蛋壳上单个气孔的平均横截面积较大。

南雄的这三种恐龙蛋的气体传导率与蒙古"原角龙"的蛋的相应值很接近，而与法国恐龙蛋的相差很多。

一、前　言

恐龙是卵生爬行动物，卵的孵化是其繁衍后代、保证物种延续的重要环节。许多研究成果已表明，恐龙的绝灭很可能与其繁殖有着密切关系（Erben, 1970; Erben, Hoeffs等 1979；赵资奎，1978；赵资奎，叶捷等，1991）。因此，进一步弄清中生代末期恐龙蛋的孵化情况，也许能为探索恐龙绝灭之谜提供有价值的参考资料。我国广东南雄盆地含有丰富的晚白垩世恐龙蛋化石，为进行这方面的研究提供了极好的条件。

与鸟蛋相似，恐龙蛋在孵化时需要通过蛋壳上密布的气孔同外界进行呼吸气体的交换，并散发水蒸汽。在整个孵化过程中，气体的流量同蛋壳结构和蛋窝中的温度、湿度及氧气和二氧化碳的含量密切相关。从生理学角度看，胚胎能够进行正常的新陈代谢，最主要地是要求蛋壳的组织结构同孵化期的微环境相适应。正是根据这一原理，Seymour 在1979年首次从法国和蒙古的三种晚白垩世恐龙蛋的蛋壳结构中推测出这些恐龙蛋都是埋藏孵化的，蛋窝微环境具有湿度高、氧气含量低和二氧化碳含量高的特点（Seymour, 1979）。稍后，Williams, Seymour 等人（1984）又研究了法国南部 Aix 盆地上白垩统地层中的四种恐龙蛋，也得出了相同的结论。

我国是世界上少数几个富含恐龙蛋化石的国家之一，已有较长的研究历史。早在六十年代中期杨钟健就根据蛋化石的外观形态对南雄盆地的恐龙蛋进行了分类（杨钟健，1965）。十年后，赵资奎按照蛋化石的显微结构重新建立了一套分类系统（赵资奎，1975）。本文即以南雄盆地的恐龙蛋化石为材料，试图采用定量研究的方法从蛋壳结构来推测恐

龙胚胎在正常发育的情况下恐龙蛋蛋窝中的微环境。文中的种属名称均引自赵的分类系统。

二、材料和方法

粤北的南雄盆地发育着一套上白垩统至下第三系的红层，其中上白垩统地层称为南雄群，岩性为紫红色的粉砂岩、砂岩和泥岩。丰富的恐龙蛋化石就产于这套地层中。

迄今为止，在南雄发现的恐龙蛋共有十二个种，分属于三个科（赵资奎，叶捷等，1991)。笔者根据蛋壳显微结构的特点，并考虑到定量研究尚需相应种的完整蛋化石，选择了瑶屯巨形蛋（*Macroolithus yaotunensis*)、粗皮巨形蛋（*M. rugustus*）和安氏长形蛋（*Elongatoolithus andrewsi*）三个种作为研究材料。其分类位置如下：

长形蛋科 Elongatoolithidae Zhao, 1975
- **巨形蛋属 *Macroolithus* Zhao, 1975**
  - **粗皮巨形蛋 *M. rugustus* Young, 1965**
  - **瑶屯巨形蛋 *M. yaotunensis* Zhao, 1975**
- **长形蛋属 *Elongatoolithus* Zhao, 1975**
  - **安氏长形蛋 *E. andrewsi* Zhao 1975**

在显微结构上，上述三个种虽然有着明显的区别，但也具有许多共同的特点(见图版 I、II 和 III)，主要表现在：气孔道比较直，不分叉，上下直径比较均匀；气孔道弦切面比较规则，近于圆形或椭圆形。此外，扫描电镜观察发现，蛋壳未受后生成岩作用的影响，仍保持原生结构(赵资奎，叶捷等，1991)。正是这些特征为定量分析提供了较大的可能性。

晚白垩世的各类恐龙蛋的结构和功能已很接近鸟蛋的组织水平，是比较进步和比较完善的(赵资奎，1979; Packard & Packard, 1980)。目前有关现生的鸟类和爬行类的卵的研究工作已取得了丰硕成果，为我们探索恐龙蛋的孵化期微环境提供了可靠的基础资料。南雄盆地的这三种恐龙蛋的显微结构已同鸟蛋的非常相似，因此笔者认为可以采用相似的研究方法。

恐龙蛋具有坚硬的钙质壳，蛋壳的通气孔道系统必须满足胚胎的两种相对要求：一方面对气体的阻碍力必须足够小，以适应胚胎对氧气的需求，保证水蒸汽、二氧化碳能及时散发；另一方面，又必须有足够大的阻碍力，以保护胚胎不至于过量失水和过量散发二氧化碳。以水分为例，现已发现鸟蛋在整个孵化期总失水量同它刚产下来时的重量的比值是一个常数（Rahn & Ar, 1974; Rahn, Paganelli 等，1976)。恐龙蛋在整个孵化过程中失水量也应该是一定的。失水量的大小又是同蛋壳的渗透结构以及蛋窝中的湿度密切相关的。我们将衡量蛋壳渗透能力大小的物理量称气体传导率（gas conductance)。基于这一原理，通过计算一定条件下蛋壳对水蒸汽和呼吸气体的传导率就可以推测出胚胎在正常发育时蛋窝中水分、氧气和二氧化碳含量的高低。

在求蛋壳的气体传导率之前，需要正确测算出以下几项有关恐龙蛋外观形态和微观结构的物理量：

1. 蛋的体积（V）和表面积（S）

为了保存恐龙蛋窝的完整性，不宜从蛋窝中取出蛋化石用埋沙等方法来测量其体积。笔者尽可能多地选择未受挤压变形的蛋在其原位测量它们的线性尺寸，利用公式（1）求出蛋的体积：

$$V = Kv \times L \times B^2 \qquad (1)$$

这一公式是 Hoyt（1979）统计了26个种共210个鸟蛋（重量范围是6.7—1692.3克）后建立的。体积系数 Kv 的平均值是 0.507±0.007(SD)。公式（1）中的L是蛋的长度（cm），B是蛋的最大宽度（cm）。

Kv 值会受到蛋的形状的影响，应加以校正后再代入公式(1)中。本文的 Kv 值都是经校正后的值。

需要说明的是，这里关于体积的计算方法同 Williams, Seymour 等人的方法不尽相同。Seymour（1979）在计算“原角龙”（*Protoceratops*）的蛋的体积时，把一个模型三分，将蛋看成是由两个半球和一个圆柱体组成。本文研究的这三种恐龙蛋的形状为长形，和“原角龙”的相似，但两端的曲率半径还是有明显差异。若采用三分法，中部不是圆柱体而是截锥体。所以本文未采用这一方法。

Williams, Seymour 等（1984）在研究法国的恐龙蛋时直接将 Kv 值取为0.51，笔者认为欠妥。恐龙蛋形状特殊，校正后的 Kv 值应高于0.51。经计算，南雄这三种恐龙蛋的 Kv 校正值是0.53—0.61。

在求出体积后，即可利用公式（2）求出表面积：

$$S = Ki \times V^{2/3} \qquad (2)$$

这里 Ki 可由公式（3）、（4）求出（Hoyt, 1976）：

$$Ki = 4.393 + 0.394El \qquad (3)$$

$$El = L/B \qquad (4)$$

El 是蛋的延长率。计算出的南雄这三种恐龙蛋的 Ki 值为5.2—5.5。Seymour(1979)直接引用 Hoyt（1976）对28种鸟蛋的统计公式，取 Ki 为4.928，而未对其进行校正。实际上，Hoyt 在同一篇文章中就指出了对于延长率较大的蛋，4.928这一 Ki 值会给表面积带来较大误差。本文的 Ki 值均是经校正后的数值。

2. 总气孔面积（Ap）

制作切于蛋壳柱状层中部的弦切面，经显微照像将气孔面积放大4300倍。由于气孔近似椭圆，笔者测量了每个气孔的长、短径，再求出它们的横截面积。对每一个种都统计了100多个气孔，最后取它们面积值的算术加权平均数作为单个气孔的平均面积。

在薄片上数出单位面积内的气孔个数。假设气孔在蛋壳上是均匀分布的，于是可知蛋壳上的总气孔数。总气孔面积等于单个气孔平均面积与总气孔数的乘积。

3. 气孔道的长度（Lp）

南雄这三种恐龙蛋壳的锥体都排列得比较紧密，气孔极少分布在蛋壳外表面突出的

瘤或棱纹上。因此，笔者将锥体底面至柱状层顶面平缓处的一段作为气孔道的长度。

求出以上几个物理量后，就可以由公式（5）求出一定温度下蛋壳对水蒸汽的传导率 G_{H_2O} [mg/(day·mmHg)]：

$$G_{H_2O} = (C/RT) \times D_{H_2O} \times (Ap/Lp) \tag{5}$$

(Ar, Paganelli 等, 1974)

这里C是转换常数 [1.56×10^9 (sec·mg)/(day·mole)] R是气体常数 [6.24×10^4(cm^3·mmHg)/(mole·°K)]，T是蛋窝中的绝对温度（°K），D_{H_2O} 是水蒸汽对空气的互渗透率（cm^2/sec）。

鸟类一般是在树上或其它空气流通的地方筑巢孵蛋，巢中的平均温度是 35—36℃ (Ar & Rahn, 1978)。爬行动物胚胎新陈代谢速率比较低，孵化温度也低一些。如位于沼泽地带的短吻鳄巢穴的平均温度是 31.1℃（Goodwin & Marion, 1978)。Seymour (1979）认为恐龙蛋的孵化温度在30℃左右，笔者也认为选择这一值是合理的，30℃下 D_{H_2O} 值为 0.292 cm^2/sec（Seymour, 1979)。

为了下文进一步的讨论，还需要估算出恐龙蛋在刚产下来时的重量。据前人资料 (Seymour, 1979; Williams, Seymour 等，1984)，恐龙蛋的比重是 1.08g/cm^3。这样，恐龙蛋的重量是：

$$W = 1.08 \times V \tag{6}$$

三、结果和讨论

1. 南雄恐龙蛋窝中的微环境特点

表1列出了南雄的三种恐龙蛋有关物理量的测算结果：

鸟蛋在刚产下来时的重量同水蒸汽传导率之间有一定的异速增长关系：

$$G_{H_2O} = 0.384 \times W^{0.841} \tag{7}$$

(Ar & Rahn, 1978)

这里 G_{H_2O} 为25℃下蛋壳对水蒸汽的传导率。将表1中三种恐龙蛋的重量代入（7）式，得到25℃下相同重量的鸟蛋的水蒸汽传导率。若不计温度造成的微小误差，所得结果分别只是表1中所列的三个G值的43%、58%和36%。

南雄恐龙蛋的如此高的水蒸汽传导率表明，它们的孵化环境与一般鸟蛋的很不相同。高传导率为胚胎在氧气少、二氧化碳多的环境中进行气体交换提供了条件，同时又与高湿度的环境相联系（Lomholt, 1976)。现生的营冢鸟和穴居鸟蛋壳的水蒸汽传导率都比较高，如澳洲火鸡（*Alectura lathami*）蛋壳的 G_{H_2O} 值是相同重量鸟蛋的2.6倍（Seymour & Rahn, 1978)。爬行动物的蛋一般都有较高的水蒸汽传导率。海龟（*Chelonia mydas*）蛋壳的平均渗透系数是鸡蛋壳的2倍（Ackerman, & Prange, 1972)；密河短吻鳄（*Alligator mississippiensis*）的蛋壳传导率比相同重量鸟蛋的高5倍（Packard, Taigen 等，1979)。因此，恐龙蛋窝中的微环境与上述几种爬行动物的蛋窝微环境相似，具有湿度很高，氧气含量低，二氧化碳含量高的特点。这样的环境极可能存在于穴坑或土堆中。可以推断，恐龙蛋是埋藏孵化的。从表1中还可看出，南雄这三种恐龙蛋的水蒸汽传导率相差

表1 南雄三种恐龙蛋的有关参量

(Table 1 Representative parameters of dinosaur eggs from Nanxiong Basin)

种名 参量		瑶屯巨形蛋 *M. yaotunensis*	粗皮巨形蛋 *M. rugustus*	安氏长形蛋 *E. andrewsi*
体积 Volume	cm^3	843±147 n = 10	548±37 n = 6	356±37 n = 8
表面积 Surface area	cm^2	474±54	354±20	274±17
重量 Weight	g	911±159	592±40	384±40
总气孔面积 Ap	cm^2	1.391	0.711	0.553
总气孔数 Pore number	个	13500	12700	8500
单一气孔面积 1 Pore area	mm^2	0.0103±0.0055 n = 131	0.0056±0.0020 n = 143	0.0065±0.0029 n = 107
气孔道长度 Pore length	mm	1.45±0.091 n = 52	1.42±0.066 n = 21	0.98±0.072 n = 35
气孔密度 Pore density	个/mm^2	0.285±0.077 n = 42	0.358±0.058 n = 37	0.310±0.089 n = 48
水蒸汽传导率 G_{H_2O}	mg/(day · mmHg)	231	120	136

不多，孵化环境是相似的。

上述结论同前人的研究成果是一致的。法国的 *Hypselosaurus*、蒙古的“原角龙”(*Protoceratops*) 和一种戈壁蜥脚类等三种恐龙的蛋壳在30℃时水蒸汽传导率分别是1203、189和17,000 mg/(day · mmHg)，各自相当于同等质量鸟蛋的7、4和100倍以上(Seymour, 1979)。法国 Aix 盆地四种类型的恐龙蛋蛋壳对水蒸汽的传导率也相当高，是同等质量鸟蛋的8—24倍 (Williams, Seymour 等, 1984)。经比较发现，南雄这三种恐龙蛋的水蒸汽传导率同“原角龙”蛋的很接近，孵化环境可能相似。这几种蛋的形状、体积和显微结构也比较相似，因此它们在恐龙蛋的系统关系上很可能是比较接近的。值得注意的是，蒙古“原角龙”蛋的时代相当于 Sentonian-Companian 期，而南雄这三种恐龙蛋的时代是相当于 Maastrichtian 期。两者时代相差两千万年左右，可是仅从它们的蛋壳结构和功能来看，都几乎没有什么区别。与此相反，南雄这三种恐龙蛋同法国南部的几种恐龙蛋和戈壁蜥脚类的蛋有较大差别，后者的蛋壳水蒸汽传导率相当高。这大概与蛋的大小和气孔道结构有关。

2. 蛋窝中的湿度

如前所述，硬质壳蛋在整个孵化期要散失一定量的水分。一般鸟蛋的总失水量是它刚产下来时重量的14—18% (Rahn & Ar, 1974; Rahn, Paganelli 等, 1976)。当失水量接近25%时，鸟类和爬行类的孵化率都会大幅度降低(Seymour, 1979)。这里假设南雄三种恐龙蛋的总失水量是它刚产下来时的重量的15%。根据 Seymour (1979) 的统计资料

（几种爬行动物的孵化期在 30℃ 时平均为 66 天）和有关现生爬行动物孵化期记录 (McIlhenny, 1934; Lynn & Brand, 1945; Goodwin & Marion, 1978)，假设 30℃ 下恐龙蛋的孵化天数为 65 天，这样可以求出蛋壳内外水蒸汽压差 ΔP_{H_2O} (mmHg)：

$$\Delta P_{H_2O} = (0.15 \times W \times 1000)/(I \times G_{H_2O}) \tag{8}$$

式中的 I 是孵化天数。计算结果见表 2。所得值比一般鸟蛋的 ΔP_{H_2O} 值 35mmHg (Rahn & Ar, 1974) 低得多。

蛋壳气室内的水蒸汽一般是饱和的，30℃ 时饱和水蒸汽压 Pi_{H_2O} 是 31.9mmHg，于是可以求出蛋窝中的水蒸汽压 Pa_{H_2O} (mmHg)：

$$Pa_{H_2O} = 31.9 - \Delta P_{H_2O} \tag{9}$$

结果见表 2。所得值同现生的穴居鸟巢中水蒸汽压 20—23 mmHg (Vleck, Vleck 等, 1983; Grant, Paganelli 等, 1984) 是相近的。从相对湿度看，普通鸟巢的平均值在 35.6℃ 时只有 45%(Rahn, Ar 等, 1979)，而南雄恐龙蛋窝在 30℃ 时已高达 60% 以上。

Seymour (1979) 将恐龙蛋在整个孵化期的最大失水量设为蛋刚产下来时的重量的 20%，并以此数计算恐龙蛋窝的相对湿度，得到的结果均在 80% 以上。一般来说，埋藏孵化的蛋失水量是比较低的。本文所假设的 15% 是指正常情况下的失水量，而不是最大值，所以计算出的相对湿度低一些。此外，除“原角龙”的蛋，Seymour 研究的其它几种恐龙蛋都具有比南雄三种恐龙蛋高得多的气体传导率，这是导致它们蛋窝中的相对湿度高达 80% 的另一重要原因。

表 2　南雄三种恐龙蛋蛋窝中的水蒸汽压和相对湿度

(Table 2　Water vapor pressures and relative humidities in dinosaur nests in Nanxiong Basin)

种名 参量		瑶屯巨形蛋 *M. yaotunensis*	粗皮巨形蛋 *M. rugustus*	安氏长形蛋 *E. andrewsi*
水蒸汽压差 (ΔP_{H_2O})	mmHg	9.1	11.4	6.5
水蒸汽压 (Pa_{H_2O})	mmHg	22.8	20.5	25.4
相对湿度 (R. H.)	%	71.5	64.3	79.6

3. 恐龙蛋对呼吸气体的传导率

恐龙蛋在失水的同时，还进行着呼吸气体的交换。运用公式 (9)—(12) 可以求出 30℃ 下蛋壳对氧气和二氧化碳的传导率 G_{O_2}、G_{CO_2} [cm³/(day · mmHg)] 以及渗透系数 K_{O_2}、K_{CO_2} [cm³/(day · cm² · mmHg)] (Vleck, Hoyt 等, 1979)：

$$G_{O_2} = 22.4/18.0 \times (D_{O_2}/D_{H_2O}) \times G_{H_2O} \tag{10}$$

$$G_{CO_2} = 22.4/18.0 \times (D_{CO_2}/D_{H_2O}) \times G_{H_2O} \tag{11}$$

$$K_{O_2} = G_{O_2}/S \tag{12}$$

$$K_{CO_2} = G_{CO_2}/S \tag{13}$$

这里 D_{O_2} 为 0.221cm²/sec，D_{CO_2} 为 0.173 cm²/sec (Paganelli, Ackerman 等, 1978)，S

表3 南雄三种恐龙蛋的呼吸气体传导率、渗透系数及蛋壳内外氧气压差

(Table 3 Conductances and diffusion coefficisions of respiratory gases and oxygen pressure differences across the eggshells of dinosaurs from Nanxiong Basin)

种名 参量		瑶屯巨形蛋 *M. yaotunensis*	粗皮巨形蛋 *M. rugustus*	安氏长形蛋 *E. andrewsi*
O_2 传导率 (G_{O_2})	$cm^3/day \cdot mmHg$	245	127	144
O_2 渗透系数 (K_{O_2})	$cm^3/(day \cdot cm^2 \cdot mmHg)$	0.52	0.36	0.53
CO_2 传导率 (G_{CO_2})	$cm^3/(day \cdot mmHg)$	192	100	112
CO_2 渗透系数 (K_{CO_2})	$cm^3/(day \cdot cm^2 \cdot mmHg)$	0.40	0.28	0.40
耗氧速率 (V_{O_2})	cm^3/h	36.9	26.9	19.6
氧气压差 (ΔP_{O_2})	mmHg	3.61	5.08	3.27

是蛋壳的表面积。结果见表3。

鸡蛋壳在37℃时渗透系数 K_{O_2}、K_{CO_2} 分别是0.276、0.216 $cm^3/(day \cdot cm^2 \cdot mmHg)$ (Wangensteen, Wilson 等, 1970/71)。南雄恐龙蛋壳的相应值大约是鸡蛋壳的1.5倍。

公式(13)表示大型爬行动物和营冢鸟的胚胎在破壳前夕最大耗氧速率 V_{O_2} (cm^3/h) 同蛋在刚产下来时的重量(W)之间的关系:

$$V_{O_2} = 0.244 \times W^{0.737} \tag{14}$$

(Sey mour, 1979)

将南雄三种恐龙蛋的重量代入(13)式求出 V_{O_2} 值,再由公式(14)求出蛋壳内外的氧气压差 ΔP_{O_2} (mmHg):

$$\Delta P_{O_2} = V_{O_2} \times 24/G_{O_2} \tag{15}$$

结果见表3。

鸟巢中鸟蛋壳内外的 ΔP_{O_2} 值一般是42mmHg (Rahn & Ar, 1980); 海龟(*Chelonia mydas*)蛋窝中蛋壳内外的 ΔP_{O_2} 是5.2mmHg (Prange & Ackerman, 1974)。南雄三种恐龙蛋的 ΔP_{O_2} 与后者接近,而比前者低得多。

总之,蛋壳的氧气渗透系数高,壳内外氧气压差低,均反映了胚胎对低氧环境的适应。

4. 导致恐龙蛋高传导率的蛋壳结构因素

南雄的这三种恐龙蛋都具有较高的气体传导率,那么究竟是什么因素导致的呢?我们试图从蛋壳结构本身来寻找答案。

鸟蛋的气孔道长度 Lp(cm)、总气孔面积 Ap(cm^2) 和气孔密度 P (个/cm^2) 同鸟蛋刚产下来时的重量 W(g) 之间分别存在着下列异速增长的关系:

$$Lp = 5.126 \times 10^{-3} \times W^{0.456} \quad (16) \quad \text{(Ar, Paganelli 等, 1974)}$$

$$Ap = 9.72 \times 10^{-5} \times W^{1.249} \quad (17) \quad \text{(Ar \& Rahn, 1978)}$$

表 4　南雄三种恐龙蛋与相同重量鸟蛋的有关量的比较

(Table 4　Comparison of dinosaur eggs from Nanxiong Basin and similarly sized bird eggs)

种　名 参　量	瑶屯巨形蛋 *M. yaotunensis*	粗皮巨形蛋 *M. rugustus*	安氏长形蛋 *E. andrewsi*
Lp/"Lp"	1.26	1.51	1.27
Ap/"Ap"	2.88	2.52	3.38
P/"P"	0.49	0.56	0.44

$$P = 279.7 \times W^{-0.231} \quad (18) \quad (\text{Ar \& Rahn, 1978})$$

由此可以计算出与这三种恐龙蛋同重的鸟蛋的蛋壳厚度“Lp”、总气孔面积“Ap”和气孔密度“P”。

从表 4 中可见，虽然实际计算的气孔道长度 Lp 比“Lp”高出 0.3—0.5 倍，但总气孔面积 Ap 却是“Ap”的 3—4 倍，这就使得最终结果——恐龙蛋气体传导率比同等重量的鸟蛋的值高出 1—2 倍。从公式 (5) 也可看出，在蛋壳结构中，决定传导率大小的因子是 Ap/Lp 这一比值。

表 4 还显示出，恐龙蛋壳的实际气孔密度 P 只是“P”的 40% 左右。因此，Ap 比“Ap”高，完全是因为单个气孔的平均横截面积大，而不是总气孔数多。鸟蛋不论质量是多少，单个气孔的水蒸汽传导率均是 1.5μg/(day · mmHg) (Ar & Rahn, 1985)，而恐龙蛋单个气孔的水蒸汽传导率是这一值的 10 倍左右。因此，可以得出结论，导致南雄恐龙蛋壳高传导率的直接因素是单个气孔的平均横截面积较大。

四、小　结

本文通过测算南雄盆地的瑶屯巨形蛋、粗皮巨形蛋和安氏长形蛋三种晚白垩世恐龙蛋的有关物理量，发现恐龙胚胎在正常发育时蛋壳有较高的气体传导率，是相同重量的鸟蛋的 2—3 倍。结论如下：

(1) 恐龙可能是挖穴或建冢孵蛋，蛋窝中的微环境具有湿度高(相对湿度达 60% 以上)、氧气含量低、二氧化碳含量高的特点。

(2) 南雄的瑶屯巨形蛋、粗皮巨形蛋和安氏长形蛋同蒙古“原角龙”的蛋在孵化期的微环境很相似。这与它们相似的形状、大小和结构是相吻合的。在恐龙蛋的系统关系上，这几种蛋可能是很接近的。不过值得注意的是，它们的分布时代相差约 20 万年，可见在这段漫长的地质时期中，这类蛋的结构和功能没有大的变化。

同法国南部的几类恐龙蛋以及蒙古的一种戈壁蜥脚类的蛋相比，南雄的这三种恐龙蛋的气体传导率低得多，这与蛋的大小和气孔道结构极有关系。

(3) 南雄恐龙蛋的气体传导率高，主要是因为单个气孔的平均横截面积大，而不是气孔道的长度和总气孔数导致的。

本文是在硕士论文一部分内容的基础上修改而成。在全文的写作中，得到了赵资奎

先生的悉心指教；张文定、段雨霞和张立波在实验室和野外工作中给予了大力帮助；陈万勇提供 OPTON 高级偏光显微镜；朱敏介绍 NCSS 统计软件；张杰冲洗图版照片；计算机室庄文露和郑芳也给予很大帮助，在此一并致谢。此外笔者还要感谢本所标本馆、广东南雄博物馆、始兴博物馆和上海自然博物馆应允测量标本。文中图版照片均为笔者拍摄。

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NEST ENVIRONMENTS OF THE LATE CRETACEOUS DINOSAUR EGGS FROM NANXIONG BASIN, GUANGDONG PROVINCE

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Key words Nanxiong Basin; Late Cretaceous; Dinosaur eggs; Nest environment; Gas conductance

Summary

As dinosaurs were oviparous animals, incubation of their eggs was the essential procedure during their reproduction. Physiologically, eggshell microstructures were bound to adapt to the nest environments during incubation if embryos normally developed. Gas conductance estimated from eggshell morphology can provide evidence for the environment conditions in nests. Seymour (1979) first estimated gas coaductance of dinosaur eggs from France and Mongolia and indicated that the nest environments of these eggs were all high in humidity, low in oxygen and high in carbon dioxide. Such conditions most likely occurred underground or within incubation mounds. Williams et al. (1984) found similar nest environments of four kinds of dinosaur eggs from Aix Basin in southern France.

Some papers about dinosaur eggs indicated that the extinction of dinosaurs would be related to their reproduction (Erben, 1970; Erben, Hoeffs et al. 1979; Zhao, 1978; Zhao, Ye et al. 1991). Thus further investigations about reproduction of dinosaurs in Late Cretaceous might be significant. This paper will reconsider the relationship between dinosaur eggs and their environments.

Material and Methods

Three "species" of dinosaur eggshells used in this study were collected from Upper Cretaceous stratigraphic horizons—Nanxiong Group in Nanxiong Basin of Guangdong Province. Up to now, 12 "species" of dinosaur eggs have been found there (Zhao, Ye et al. 1919). However, only three of them have complete fossil eggs available to measure their sizes. The taxa of the three "species' are shown as follows:

Elongatoolithidae Zhao, 1975
***Macroolithus* Zhao, 1975**
***Macroolithus yaotunensis* Zhao, 1975**
***Maroolithus rugustus* Young, 1965**
***Elongatoolithus* Zhao, 1975**
***Elongatoolithus andrewsi* Zhao 1975**

Although the three "species" can be distinguished easily from their microstructures, there are still many similarities among them (see Plate I, II, III): The pore canals are straight and unbranched; The cross sections of pores are regular and appear circles or ovals. These characteristics make it possible for us to measure shell and pore geometry to estimate the gas conductance through the shell.

The structures and functions of the dinosaur eggs in Late Cretaceous are advanced and have approached the levels of living bird eggs (Zhao, 1979; Packard & Packard, 1980). The microstructures of the three "species" studied here are very similar to those of bird eggs. So it is reasonable to use similar research methods.

The dinosaur eggs had rigid calcareous shells as significant resistances to diffusion of water vapor and respiratory gases. The porosity of shell had to satisfy embryo's two opposite metabolic requirements: providing adequate exchange of respiratory gases between the embryo and its environment and limiting evaporative water loss.

In bird eggs, the percentage of water loss during incubation to the initial weight is always a constant (Rahn & Ar, 1974; Rahn, Paganelli et al. 1976). There is a good reason to believe that the dinosaur eggs were the same case. The quantity of gas which diffuses per unit of time through the whole egg shell under a unit of partial pressure difference is defined as gas conductance (symbolized by G). By the conductance of water vapor and respiratorp gases on certain conditions, we can estimate the humidityand the concentrations of oxygen and carbon dioxide in the dinosaur nests. Before estimating the gas conductances, we have to know the values of the following parameters about sizes and microstructures of the dinosaur eggs:

1. Volume (V) and Surface Area (S) of the Egg

Some undeformed eggs were selected to measure their linear dimensions in nests to estimate their volumes by Eq. (1):

$$V = Kv \times L \times B^2 \qquad (1)$$

This is an empirical formula of bird eggs (Hoyt, 1979). L is the length of egg, B is the breadth, Kv is the index of volume. The mean Kv is 0.507+0.007 (SD) for bird eggs whose initial weights range from 6.7 to 1692.3g. Because of the systematic effect of shape on Kv, the values of Kv used in the present paper are all corrected for the dinosaur eggs, ranging from 0.53 to 0.61.

The method of calculating egg volume here is different from that by Seymour (1979), who estimated the volume of the "*Protoceratops*" egg from linear measurements of a cast and assumed the original egg to consist of a cylindrical portion capped with two hemispheres. The three "species" of dinosaur eggs studied here are also elongated eggs, but the sizes of their two ends are quite different.

The relationship between volume and surface area is.

$$S = Ki \times V^{2/3} \tag{2}$$

Ki is the Surface-Volume Index. It is highly correlated with Elongation of the egg (Hoyt, 1979):

$$Ki = 4.393 + 0.394El \tag{3}$$

$$El = L/B \tag{4}$$

Corrected by the two equations, the Ki values of the three "species" of the dinosaur eggs studied here are 5.2—5.9.

2. Total Pore Area (Ap)

More than 100 pores for each "species" were selected at random to measure their areas. Each pore area was photographically enlarged 4300 times. As the pores are often not circles but ovals, the area of each one is determined by the measurements of its major and minor axes. The average individual areas of pores of the three "species" are shown in Table 1.

The pores in a unit area of the tangential thin-sections were counted with microscope. Assuming an even distribution of pores, the total number and area of pores in egg shell are easily known.

3. Length of Pore Canal (Lp)

Length of pore canal greatly affects the diffusion of gas. In the three "species" from Nanxiong Basin, the cones arrange closely and probably provide effective resistance to diffusion. It is also found that the pores are rarely exposed on the tubercles. So the effective pore length is determined from the bottom of cone to the plane top of column in radial thinsections.

Water vapor conductance through the eggshell can be estimated by Eq. (5) from measurements mentioned above (values presented in Tablt 1):

$$G_{H_2O} = (C/RT) \times D_{H_2O} \times (Ap/Lp) \tag{5}$$

(Ar, Paganelli et al. 1974)

Here C is a conversion constant 1.56×10^9 [(sec·mg)/(day mole)], R is the gas constant 6.24×10^4[(cm^3·mmHg)/(mole·°K)], This the absolute temperature in nest during incubation (°K), D_{H_2O} is binary diffusicity (cm^2/sec).

The incubation temperature in bird nests is usually 35—36°C (Ar & Rahn, 1978). As the metabolic rates of reptilian embryos are lower than those of avian embryos, the incubation temperatures also seem to be lower. For example, the nests of alligators living in marshland have a mean temyerature of 31.1°C (Goodwin & Marion. 1978). Seymour (1979) assumed the dinosaur eggs hatched at temperatures around 30°C when the incubation time was 66 days. Here the temperature in the dinosaur nests in Nanxiong Basin is also assumed to be 30°C. D_{H_2O} is 0.292 cm^2/sec at 30°C (Seymour, 1979).

Assuming that fresh dinosaur eggs had a density similar to that of recent bird eggs (1.08 g/cm^3), their weights may be calculated according to Eq. (6) (Paganelli et al. 1974):

$$W = 1.08 \times V \tag{6}$$

Results and Discussion

1. Characteristics of the Nest Environmente

The values of representative parameters of the three "species" of the dinosaur eggs from

Nanxiong Basin are presented in Table 1. It is known that there is an allometric relationship for bird eggs between the fresh weight and water vapor conductance through the eggshell:

$$G_{H_2O} = 0.384 \times W^{0.841} \text{ (Ar \& Rahn, 1978)} \qquad (7)$$

Here G_{H_2O} is water vapor conductance at 25°C. According to Eq. (7), the three "species" of dinosaur eggs from Nanxiong Basin predict G_{H_2O} to be only 43%, 58% and 36% of measured values, respectively (The effect of temperature is negligible).

The high conductance of water vapor through the dinosaur eggshells studied here indicates that their nest environments were far different from those of birds. The highly porous eggshells always make it possible for embryos to exchange gases in the hypoxic and hypercapnic environment with high humidity (Seymour and Rahn, 1978; Lomholt, 1976). The eggs of recent megapode or burrowing birds show high gas conductance. For example, the G_{H_2O} in eggs of the Australian Brush Turkey (*Alectura lathami*) is 2.6 times higher than that in similarly sized bird egg hatching above ground (Seymour & Rahn, 1978). Reptilian eggs usually show high gas conductance. The average diffusion coefficision in eggs of *Chelonia mydas* is two times that in hen's eggs (Ackerman & Prange, 1972); *Alligator mississippiensis* shows gas conductance 5 times higher than that in the bird egg which has the same weight (Packard, Taigen et al. 1979). Therefore, like the nest environments of other reptiles, the nests of the three "species" of dinosaur eggs in Nanxiong Basin were high in humidity, low in oxygen and high in carbon dioxide. Such conditions most likely occurred underground or within mounds. It is reasonable to draw a conclusion that the dinosaurs in Nanxiong Basin probably buried their eggs for incubation. Table 1 shows that the water vapor conductances in the three "species" have few differences each other and their nest environments might be similar.

According to Seymour (1979) and Williams et al. (1984), G is 1203, 189 and 17,000mg/(day·mmHg) at 30°C in the eggshells of *Hypselosaurus* from France, "*Protoceratops*" from Gobi Desert in Mongolia and a Gobi sauropode respectively, and the values are over 7,4 and 100 times higher than predicted (Seymour, 1979). The dinosaur eggs from Aix Basin in southern France show gas conductances 8—24 iimes higher than those of similarly sized bird eggs (Williams, Seymour et al. 1984).

As shown above, there is strong resemblance between water vapour conductances in the eggs from Nanxiong Basin and in the eggs of "*Protoceratops*" from Mongolia. This indicates that their nest environments might be similar. These "species" are probably close in taxonomical positions because their shapes, sizes and shell microstructures are similar too. However, it should be noticed that the geological time of the three "*species*" from Nanxiong Basin is Maastrichtian while the time of "*Protoceratops*" is Sentonia-Campanian. It shows that there were very few changes in structures or functions of the dinosaur eggs during about 20 million years.

The gas conductances in the three "species" of eggs from Nanxiong Basin differ markedly from those in the Gobi saurpode eggs from Mongolia and in all kinds of eggs from southern France. The latter are much higher perhaps because the eggs are larger in size and higher in porosity.

2. Humidity In Dinosaur Nest

As mentioned above, the water loss of a bird egg during incubation is always 14—18% of its initial weight (Rahn & Ar, 1974; Rahn, Paganelli et al. 1976). In both birds and reptiles, hatchability will decline sharply if water loss approaches 25% (Seymour, 1979). On this basis, I assumed water loss for the dinosaur eggs from Nanxiong Basin normally of 15%. According to the present statistical data about incubation time of some living reptiles (McIlhenny, 1934; Lynn & Brand, 1945; Goodwin & Marrion, 1978; Seymour, 1979), the incubation tim e(I) for dinosaur eggs might be 65 days at 30°C. Thus the vapor pressure difference across the shell ΔP_{H_2O} (mmHg) is:

$$\Delta P_{H_2O} = (0.15 \times W \times 1000)/(I \times G_{H_2O}) \tag{8}$$

It is shown in Table 2 that values of ΔP_{H_2O} are all much lower than 35mmHg which is the vapor pressure difference across bird eggshell in nest (Rahn & Ar, 1974).

The air cell in egg is completely saturated, and water vapor pressure is 31.9mmHg in it. Then the external water vapor pressure Pa_{H_2O} is:

$$Pa_{H_2O} = 31.9 - \Delta P_{H_2O} \tag{9}$$

The values of Pa_{H_2O} presented in Table 2 are similar to those of burrowing bird nests with about 20—23mmH gR.H. (Vltck, Vleck et al. 1983; Grant, Paganelli et al. 1984). In relative humidity, bird nests above ground are 45% at 35.6°C (Rahn, Ar et al. 1979) while the dinosaur nests in Nanxiong Basin are more than 60% at 30°C.

As Seymour (1979) assumed the tolerance to dehydration in dinosaur eggs is about 20% of the initial egg weight and took it into Eq. (8), the relative humidities in the nests are more than 80%. The water loss of 15% in the present paper is assumed the normal one, not the maximum. So the humidities in nests in Nanxiong Basin are lower than those estimated by Seymour (1979).

3. Conductances of Respiratory Gases Across Dinosaur Eggshells

Dinosaur embryos exchanged oxygen and carbon dioxide with external atmosphere across the shells. It is easily to know the conductance and diffusion coefficision of respiratory gases by Eq. (10)—(13) (Vleck, Hoyt et al. 1979).

$$G_{O_2} = 22.4/18.0 \times (D_{O_2}/D_{H_2O}) \times G_{H_2O} \tag{10}$$

$$G_{CO_2} = 22.4/18.0 \times (D_{CO_2}/D_{H_2O}) \times G_{H_2O} \tag{11}$$

$$K_{O_2} = G_{O_2}/S \tag{12}$$

$$K_{CO_2} = G_{CO_2}/S \tag{13}$$

Here D_{O_2} is 0.221cm^2/sec, D_{CO_2} is 0.173cm^2/sec (Paganelli, Ackerman et al. 1978), S is the surface area of the egg shell. The results are presented in Table 3.

The diffusion coefficisions K_{O_2} and K_{CO_2} in hen's eggs are 0.276, 0.216cm^3/(day·cm^2·mmHg) respectively (Wangensteen, Wilson et al. 1970/71). Values of K_{O_2} and K_{CO_2} in the dinosaur eggs from Nanxiong Basin are about 1.5 times of them.

The following Eq. (14) shows the relationship between the prehatching oxygen consumption (V_{O_2}) of embryo and the initial egg weight for large reptiles and birds nesting underground (Seymour. 1979):

$$V_{O_2} = 0.244 \times W^{0.737} \tag{14}$$

This equation is used to predict V_{O_2} in the three "species" from Nanxiong Basin. According to Eq. (14), the oxygen pressure difference across the shell ΔPO_2 (mmHg) can be estimated:

$$\Delta P_{O_2} = V_{O_2} \times 24/G_{O_2} \tag{15}$$

The values are shown in Table 3.

ΔPO_2 is usually 42mmHg in bird nests (Rahn & Ar, 1980), and 5.2mmHg in the nest of *chelonia mydas* (Prange & Ackerman, 1974).

ΔPO_2 in dinosaur nest is much lower than the former and similar with the latter.

To sum up, the high oxygen coefficisions for the dinosaur eggshells and low oxygen partial pressure differences across the shells are evidences for hypoxic environments.

4. Factors on Shell Structures Causing High Gas Conductance

All the three "species" of dinosaur eggs from Nanxiong Basin show high gas conductances. It seems to be interesting to find out the reasons.

In bird eggs there is the following allometric relationships between the initial egg weight W and the shell thickness Lp, total pore area Ap and pore density P respectively:

$$L_P = 5.126 \times 10^{-3} \times W^{0.456} \text{ (Ar, Paganelli et al. 1974)} \quad (16)$$

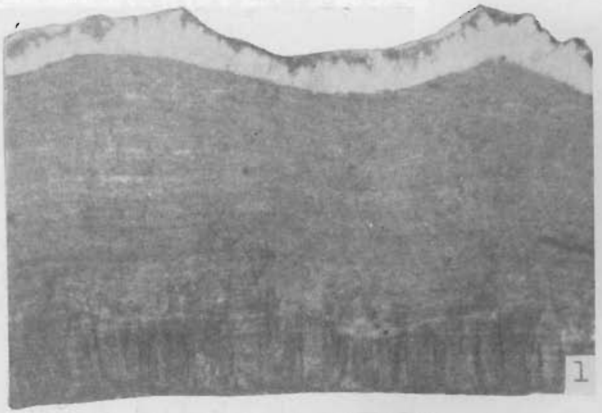
$$A_p = 9.72 \times 10^{-5} \times W^{1.249} \text{ (Ar \& Rahn, 1978)} \quad (17)$$

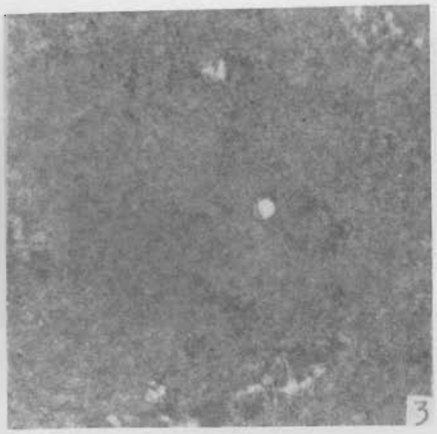
$$P = 279.7 \times W^{-0.231} \text{ (Ar \& Rahn, 1978)} \quad (18)$$

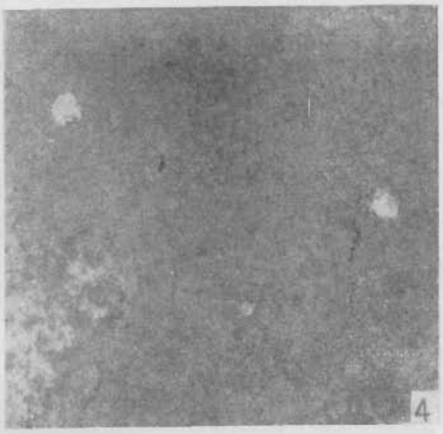
Accordingly, we can know the predicted values of "LP", "AP" and "P" in bird eggs which have the same weights with dinosaur eggs from Nanxiong Basin (see Table 4).

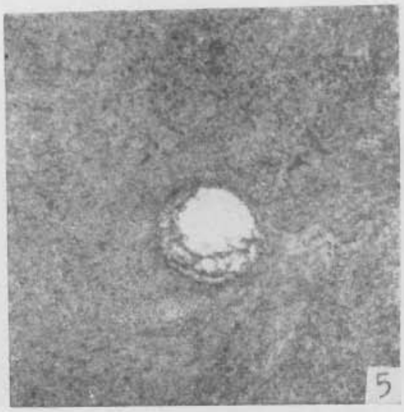
From Table 4, we can see that the dinosaur eggshells are thicker than those of similarly sized bird eggs on the one hand, on the other hand, the total pore areas of the former are about 3 times higher. As a result, the values of G are still higher. Because the measured pore densities of dinosaur eggshells are only 40% of the predicted, the large total pore areas are completely due to the large individual pore area, rather than the number of pores. Water vapor conductance across the individual pore in the dinosaur eggs is 10 times that in bird eggs which is 1.5μg/(day·mmHg) no matter how much the egg mass is (Ar & Rahn, 1985).

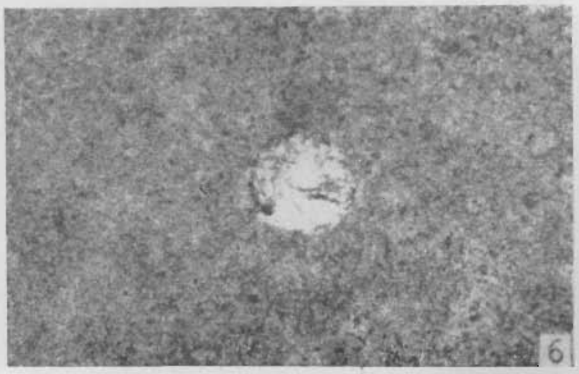
Therefore, the high water vapor conductance of the specimens from Nanxiong Basin is mainly dependent on large individual pore area, not the number of pores in the shell.





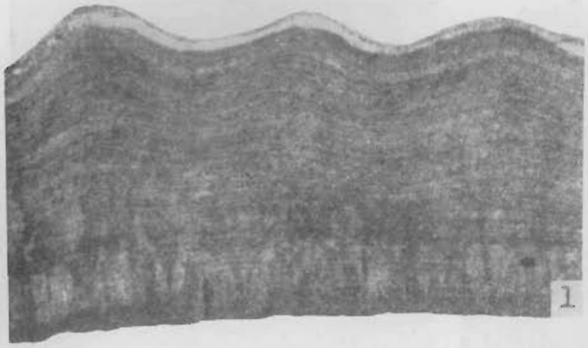


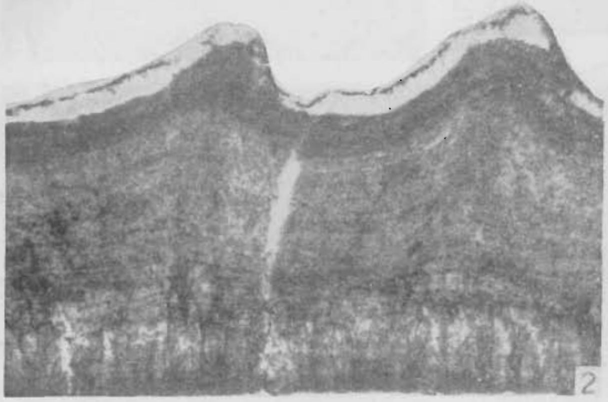


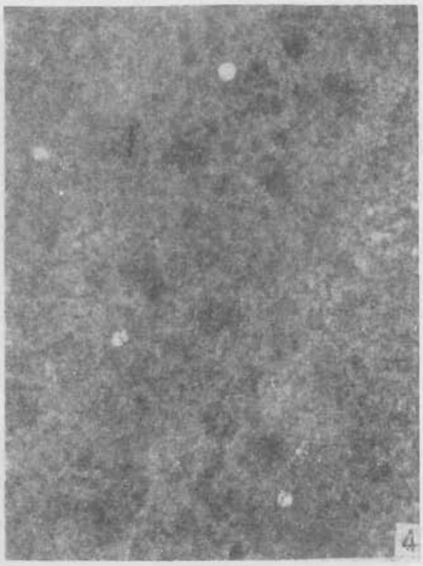


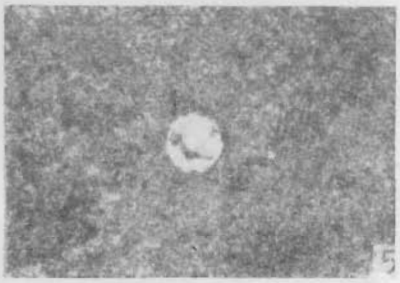
瑶屯巨形蛋（***Macroolithus yaotunensis***）

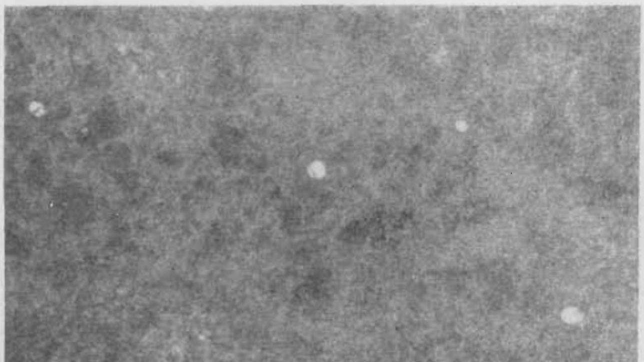
1.蛋壳径切面（radial section of eggshell), CGF-II, ×27　2.蛋壳径切面（radial section of eggshell), CGN-Pl, ×27　3.蛋壳弦切面,示三个气孔（tangential section of eggshell, showing three pores), CGN-Pl, 27×27　4.蛋壳弦切面,示三个气孔（tangential section of eggshell, showing three pores), CGN-Pl, 27×27　5.气孔横截面（cross-section of a pore), CGN-Pl, 106×106　6.气孔横截面（cross-section of a pore), CGN-Pl, 106×106

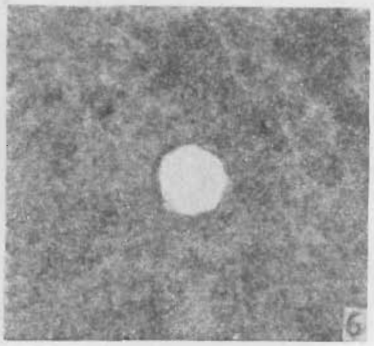






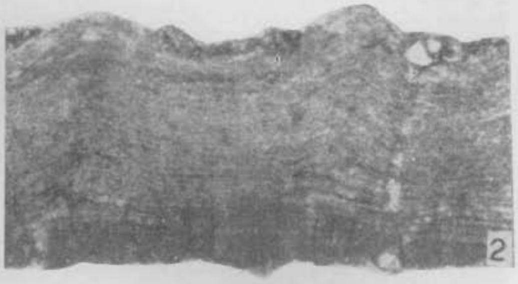


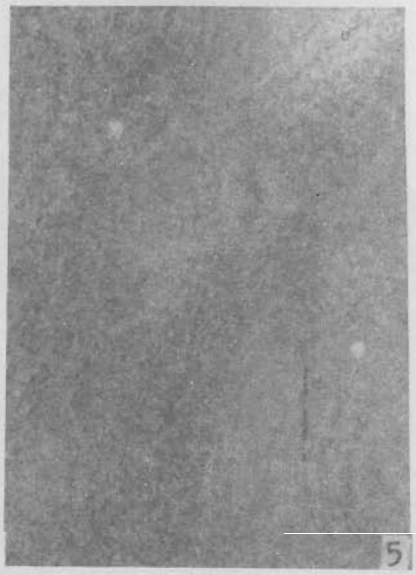


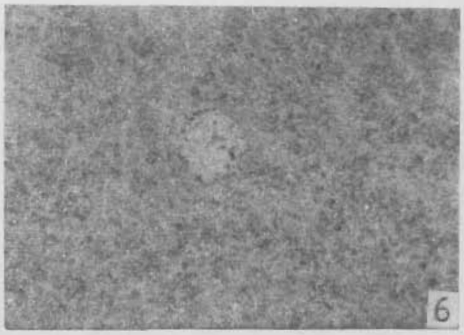


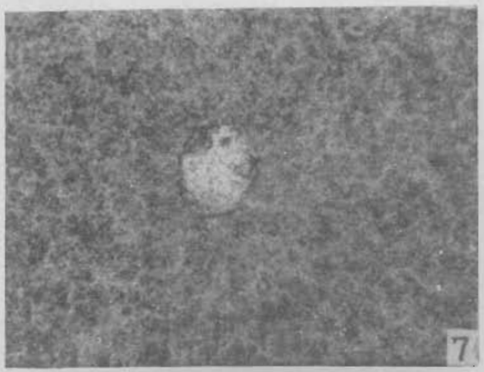
粗皮巨形蛋（*Macroolithus rugustus*）

1.蛋壳径切面 (radial section of eggshell), 6223, ×27 2.蛋壳径切面 (radial section of eggshell), 6223, ×27 3.蛋壳弦切面，示五个气孔 (tangential section of eggshell, showing five pores), 6223, 27×27 4.蛋壳弦切面,示四个气孔 (tangential section of eggshell, showing five pores), 6223, 27×27 5.气孔横截面 (cross-section of a pore), 6223, 106×106 6.气孔横截面 (cross-section of a pore),6223, 106×106









安氏长形蛋（*Elongatoolithus andrewsi*）

1. 蛋壳径切面（radial section of eggshell），CGX-1，×27　2. 蛋壳径切面，示气孔道（radial section of eggshell, showing a pore canal），CGY-1，×27　3. 蛋壳径切面，示锥间空隙（radial section of eggshell, showing space between cones），CGY-1，×27　4. 蛋壳径切面（radial section of eggshell），CGD-2，×27　5. 蛋壳弦切面，示两个气孔（tangential section of eggshell, showing two pores），CGY-1，27×27　6. 气孔横截面（cross-section of a pore），CGY-1，106×106　7. 气孔横截面（cross-section of a pore），CGY-1，106×106