中国白垩纪蜂窝蛋化石的分类订正[1)]

张蜀康
(1 中国科学院古脊椎动物与古人类研究所,脊椎动物进化系统学重点实验室 北京 100044)
(2 中国科学院研究生院 北京 100049)

摘要:重新系统描述了蜂窝蛋科蜂窝蛋属的模式蛋种宁夏蜂窝蛋(*Faveoloolithus ningxiaensis*)和杨氏蛋属的模式蛋种夏馆杨氏蛋(*Youngoolithus xiaguanensis*),并记述了产自浙江天台的蜂窝蛋科新材料,建立一个新的蛋属——副蜂窝蛋属(*Parafaveoloolithus*),及3个新的蛋种——*Parafaveoloolithus microporus*,*P. macroporus* 和 *P. tiansicunensis*。根据赵资奎1994年提出的恐龙蛋分类中具有鉴定意义的几个特征,重新讨论了现有蜂窝蛋的分类地位,提出杨氏蛋属应当提升为科一级的分类单元,总结了蜂窝蛋科内属级和种级分类单元的主要鉴定特征以及蜂窝蛋类的鉴定方法。

关键词:浙江天台盆地,晚白垩世,蜂窝蛋类,分类学
中图法分类号:Q915.21 **文献标识码**:A **文章编号**:1000-3118(2010)03-0203-17

蜂窝蛋化石最早发现于蒙古北戈壁的Ologoy-Ulan-Tsav高地,Sochava (1969)对其蛋壳的显微结构进行了研究,将其命名为多孔蛋壳(multicanaliculate),地质时代为早白垩世—晚白垩世。20世纪70年代初期,在我国内蒙古阿拉善左旗(当时归属于宁夏回族自治区)首次发现蜂窝蛋化石。这些蛋化石近乎圆形,在蛋窝中的排列方式无规律,蛋壳径切面中分布有无数直管状的气孔道。根据赵资奎(1975)提出的恐龙蛋化石分类和命名方法,赵资奎、丁尚仁(1976)将其命名为宁夏蜂窝蛋(*Faveoloolithus ningxiaensis*),并建立了蜂窝蛋科(Faveoloolithidae)和蜂窝蛋属(*Faveoloolithus*),其时代为早白垩世—晚白垩世。1979年,在河南内乡夏馆盆地又发现一窝蛋化石。其蛋壳显微结构与宁夏蜂窝蛋的很相似,但气孔道大多数分枝;蛋化石形状为橄榄形,在蛋窝中的排列方式有一定规律。赵资奎认为该标本应为蜂窝蛋类一新的蛋属、蛋种,命名为夏馆杨氏蛋(*Youngoolithus xiaguanensis*),其时代被定为白垩纪(赵资奎,1979a)。

从1979年至今,在我国河南的淅川、西峡(周世全、韩世敬,1993;张玉光、李奎,1998)和五里川(周世全、冯祖杰,2002)等盆地,浙江的金衢、天台(张玉光、李奎,1998)和永康盆地(俞云文等,2003)以及湖北郧县的青龙山地区(关康年等,1997;周修高等,1998)均有蜂窝蛋化石的报道。另外,在蒙古国的Khermiyn-Tsav, Ikh-Shunkht (Mikhailov et al., 1994)

1) 国家自然科学基金项目(编号:40772017)资助。
收稿日期:2009-11-20

和韩国南部的宝城(Huh and Zelenitsky, 2002)也发现成窝保存的蜂窝蛋化石。但是,除我国西峡盆地的一些蛋化石被命名为西坪杨氏蛋(*Youngoolithus xipingensis*)外(方晓思等,1998, 2007), 其他的大多被鉴定为蜂窝蛋属的成员,并未定种,有些只是被归为蜂窝蛋科。

可以看出,尽管蜂窝蛋化石的分布范围比较广,数量也很多,但研究程度并不高,有许多新类型还有待鉴定。赵资奎在研究蜂窝蛋属和杨氏蛋属的模式蛋种宁夏蜂窝蛋和夏馆杨氏蛋时,由于条件的限制,不能清楚地观察蛋壳的显微结构,以为它们是由一层方解石微晶叠积而成(赵资奎、丁尚仁,1976; 赵资奎,1979a)。直到用扫描电镜观察了杨氏蛋的蛋壳之后,才发现蜂窝蛋类的蛋壳也是由叠覆生长的壳单元组成(Zhao, 1994)。如今的设备与技术条件相比于20世纪70年代有了巨大的进步,运用现在的普通光学显微镜和偏光显微镜可以更清楚地观察到蜂窝蛋类的蛋壳显微结构。因此,本文将对宁夏蜂窝蛋和夏馆杨氏蛋以及浙江天台盆地发现的新材料进行更深入的形态学研究及分类订正。

1 研究材料及方法

1.1 材料

1) 宁夏蜂窝蛋 *Faveoloolithus ningxiaensis* Zhao & Ding, 1976, IVPP V 4709,一窝共11枚蛋,为赵资奎、丁尚仁(1976)描述的正型标本;一枚破损的蛋,IVPP V 16856。

2) 夏馆杨氏蛋 *Youngoolithus xiaguanensis* Zhao, 1979, IVPP V 5783, 一窝共16枚蛋,为赵资奎(1979)描述的正型标本。

3) 20世纪70年代浙江区测队在天台县方山采集的两枚不完整蛋,IVPP V 16857.1–2。

4) 2007年本文作者与同事王强等在浙江省天台县赖家村北,方山脚下采集到的标本,IVPP V 16858, 由一窝蛋上取下的碎蛋壳。

5) 20世纪90年代,蒋严根和赵宏在浙江省天台县田思村采集到的碎蛋壳,IVPP V 16859。

以上标本均保存于中国科学院古脊椎动物与古人类研究所,下文中简以"V"字号表示。

1.2 方法

蛋化石的分类方法 在正确理解蛋壳基本组织结构及其形成机制的基础上,根据赵资奎(1975, 1979b, 1994)提出的恐龙蛋分类和命名方法,判断上述材料在蛋化石宏观形态、蛋壳显微结构和蛋窝结构上的差异,并据此确定它们的分类地位。

组织切片的制备 在宁夏蜂窝蛋的蛋窝中挑选几枚蛋,每枚蛋上取1–2块蛋壳碎片;在夏馆杨氏蛋的蛋窝中挑选几枚蛋,每枚蛋在端部和中部各取一块蛋壳碎片。在编号为V 16857.1 的蛋化石上取4块蛋壳碎片。在V 16858 和V 16859 中分别挑选2–3块保存较好的蛋壳碎片。

将蛋壳碎片用树脂包埋好并固化,每一份样品中部分碎片沿径切面方向切开,部分碎片沿弦切面方向切开。把切好的样品粘在载玻片上,用切片机切下厚度约为 100 μm 的薄片,再用砂纸将薄片磨至大约 30 ~ 40 μm 厚,用树脂封片后在 Leica DMRX 型偏光显微镜下观察。

2 系统描述

本文的描述术语采用赵资奎(1994)和佘德伟(1995)建立的蛋壳术语方案。

蜂窝蛋科 Faveoloolithidae Zhao & Ding, 1976

修订特征 蛋化石圆形或椭圆形,外表面光滑。蛋壳由一层壳单元,或 2-3 个重叠生长的壳单元组成。从弦切面观察,总体为蜂窝状结构。气孔道多数较直且少分枝。

蜂窝蛋属 *Faveoloolithus* Zhao & Ding, 1976

修订属征 见模式蛋种宁夏蜂窝蛋的修订特征。

宁夏蜂窝蛋 *Faveoloolithus ningxiaensis* Zhao & Ding, 1976

(图 1,2)

正型标本 一窝共 11 枚蛋。野外地点编号 73032, 标本编号 IVPP V 4709。

归入标本 一枚残破的蛋化石,野外地点编号 S202, 标本编号 IVPP V 16856。

地点和层位 内蒙古阿拉善左旗巴音乌拉山查汗敖包大冲沟两岸白垩系的紫红色含砾粗砂岩中(赵资奎、丁尚仁,1976)。

修订特征 蛋化石近圆形,在蛋窝中的排列方式无规律。蛋壳由 2-3 个长短不一的壳单元重叠而成。壳单元粗大,呈锥形,生长纹发育,在近内表面处相互间不分离。

描述 正型标本为一窝共 11 枚蛋,其中有两枚一侧风化得比较严重,另有一枚仅残留了一小半。总体看来,蛋化石在蛋窝中排列得比较均匀,蛋之间的间距在 10 ~40 cm 左右,各个蛋化石埋藏的位置不在同一平面上(图 1)。值得注意的是那枚残留了一小半的蛋化石,它直接叠覆在另一枚蛋化石上,说明这窝蛋化石原来应当不止一层,因此不能代表一整窝蛋。

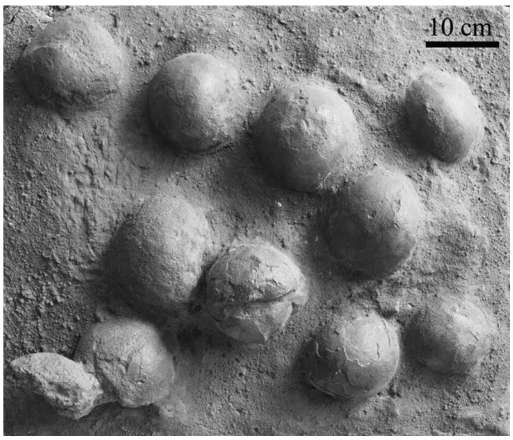

图 1 宁夏蜂窝蛋,V 4709

Fig. 1 *Faveoloolithus ningxiaensis*, V 4709

蛋化石长径为 130. 8 ~143. 7 mm, 平均 133.6 mm; 最大横径为 117.6 ~127. 9 mm, 平均 120. 3 mm; 形态指数(最大横径/长径×

100)为 90.0 ~95.0, 平均 92.7, 表明它们近似圆形。

从蛋的排列方式上看,除去残留了一小半的那枚蛋化石外,仅有 3 枚的长轴大致是指向同一方向,其他蛋化石的长轴方向是随机的,表明它们在窝内的排列方式没有一定的规律。

蛋化石外表面光滑,局部存在风化作用造成的浅坑和不规则形凹槽,蛋壳厚度为 1.20 ~1.54 mm, 平均 1.40 mm。从径切面上看,蛋壳通常由 2-3 个长短不一的壳单元叠加一起,由里向外延伸至蛋壳外表面而组成,某些部位仅由一个壳单元组成。在单个壳单元内,放射状结构比较发育,生长纹呈略向蛋壳外表面凸起的弧形。蛋壳中密布着贯通内外表面的气孔道。它们多数较直,并且少有分枝(图 2A, A')。

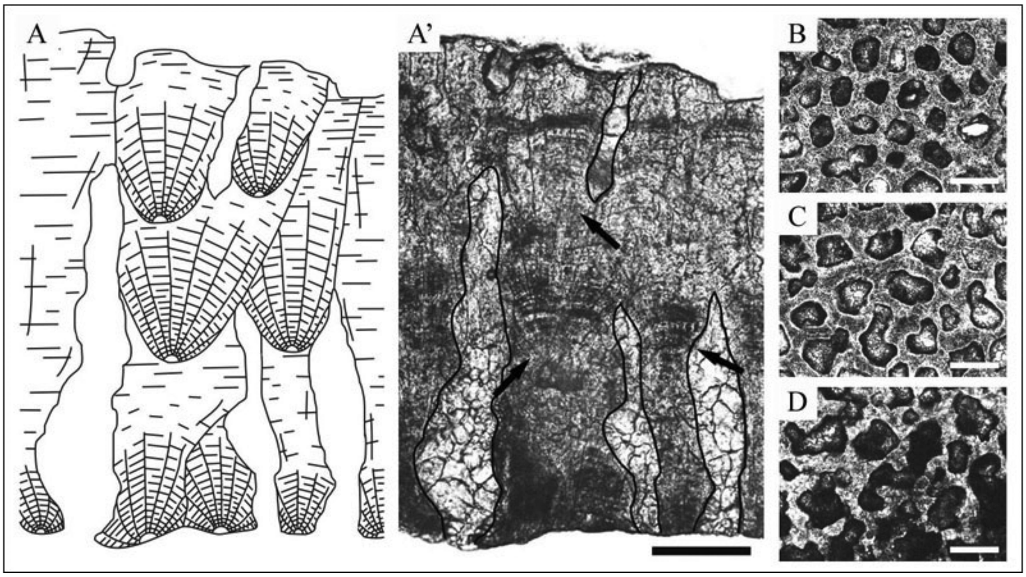

图 2 宁夏蜂窝蛋蛋壳显微结构,V 4709

Fig. 2 Eggshell microstructure of *Faveoloolithus ningxiaensis*, V 4709

A, A'. 径切面,箭头示叠覆生长的壳单元,照片中的黑色曲线示气孔道的轮廓 radial view, note superimposed shell units (arrows) and pore canals (black curves in the photo), A. 线条图 line drawing, A'. 照片 photo; B. 近外表面处弦切面 tangential view near outer surface of eggshell; C. 蛋壳中部弦切面 tangential view in middle part of eggshell; D. 近内表面处弦切面 tangential view near inner surface of eggshell; 比例尺 scale bars = 300 μm

从弦切面上看,蛋壳总体结构为蜂窝状,气孔大多数近圆形。近外表面处气孔直径较小(图 2B), 稍向内,气孔直径略增大并保持稳定。蛋壳中部的弦切面上气孔直径为 0.07 ~ 0.40 mm, 平均 0.20 mm, 气孔密度为 18 个/mm^2, 并开始出现少数形态不规则的气孔(图 2C)。向内表面方向不规则的气孔逐渐增多,相邻的气孔开始出现合并的趋势。至近内表面处大多数气孔的形态很不规则,但气孔道壁基本完整,整体结构仍为蜂窝状(图 2D)。

讨论 赵资奎、丁尚仁(1976)最初观察宁夏蜂窝蛋的蛋壳径切面时,因技术条件所限,没有发现蛋壳内的锥体,因而没有观察到壳单元的存在,以为这些蛋壳是由一层均一

的方解石微晶所组成。通过本文的研究发现,宁夏蜂窝蛋的蛋壳内分布着许多排列不甚规则的叠覆生长的壳单元,它们侧向联合在一起,组成蜂窝状结构,表明宁夏蜂窝蛋蛋壳的生长方式与一般常见的由锥体层和柱状层组成的蛋壳完全不同,在最初形成的壳单元上又继续生长出新的壳单元,从而形成完整的蛋壳结构。

副蜂窝蛋属(新蛋属) *Parafaveoloolithus* oogen. nov.

词源　Para-, 源自希腊语 *para*, 意为“近,旁,并行”; -faveoloolithus, 来自宁夏蜂窝蛋的属名 *Faveoloolithus*。

模式蛋种　*Parafaveoloolithus microporus* oosp. nov.。

属征　蛋化石圆形或椭圆形。蛋壳常由一层壳单元组成,少数部位由 2–3 个壳单元重叠而成。壳单元柱状,形态不完整,生长纹不发育,在近内表面处相互分离。壳单元内棱柱体之间界线清晰。

小孔副蜂窝蛋(新蛋种) *Parafaveoloolithus microporus* oosp. nov.

(图 3,4)

词源　种名 *microporus* 意为“小孔”,表明该种蛋化石气孔直径小。

正型标本　一枚压扁的不完整蛋,野外地点编号 No. 45, 标本编号 IVPP V 16857.1。

归入标本　另一枚不完整蛋,野外地点编号 No. 45, 标本编号 IVPP V 16857.2。

地点和层位　浙江省天台县方山,赖家组红色泥岩中,上白垩统。

特征　蛋化石近圆形,蛋壳通常由一层长柱状壳单元组成,少数部位由两个壳单元重叠在一起组成。锥体特别细小。气孔道窄且密度大。

描述　V 16857.1 近圆形,长径为 141.06 mm, 最大横径为 129.44 mm (因化石不完整而略偏小),形态指数 91.8; V 16857.2 的长径为 149.12 mm (图 3)。蛋壳外表面光滑,厚度为 2.20 ~ 2.35 mm。

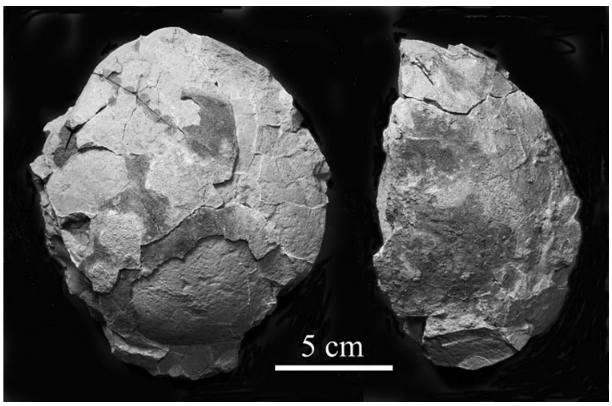

图 3　小孔副蜂窝蛋(新蛋种),V 16857.1 (左,正型标本), V 16857.2(右)

Fig. 3　*Parafaveoloolithus microporus* oosp. nov., V 16857.1(left, holotype); V 16857.2(right)

蛋壳通常由一层长柱状壳单元组成,少数部位由两个壳单元重叠在一起组成。单个壳单元中锥体很不明显,放射状结构很不发育;棱柱体之间界线清晰,生长纹不发育。蛋壳径切面上气孔道大多数直而不分枝,且非常密集(图 4A, A’)。

弦切面上蛋壳结构为蜂窝状,气孔大多数近圆形,少数形态不规则(图 4B,C)。蛋壳中部气孔直径变异范围为 0.06 ~ 0.25 mm,平均值为 0.15 mm,气孔密度为 35 个/mm^2。从蛋壳中部开始,越接近内表面,形态不规则的气孔越多,气孔道直径也

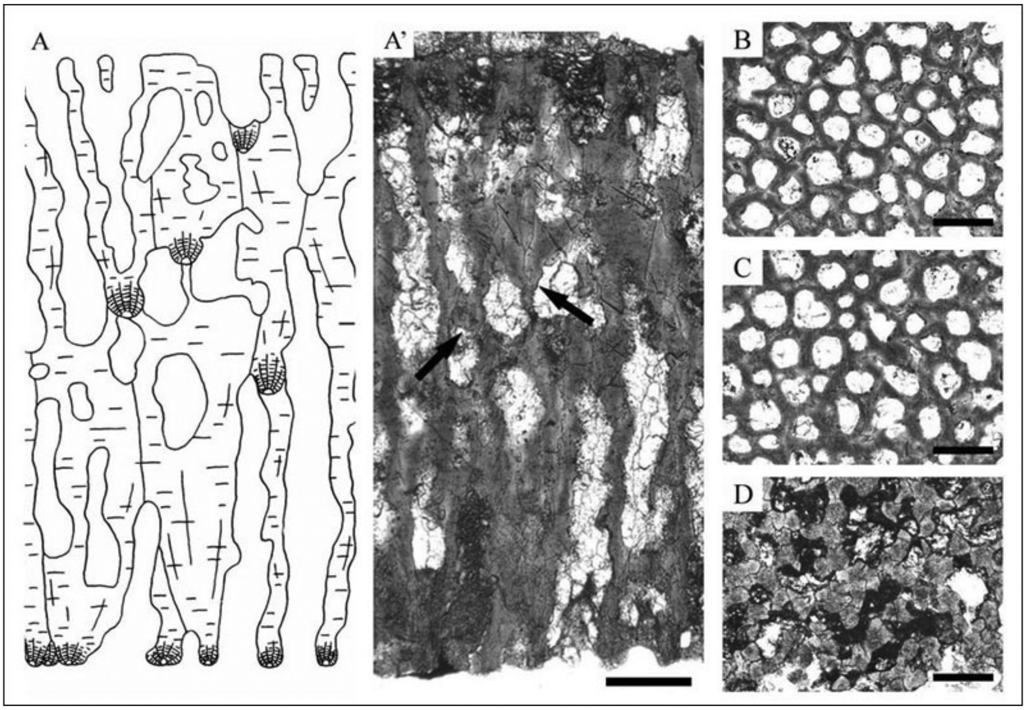

图 4 小孔副蜂窝蛋(新蛋种)蛋壳显微结构,V 16857.1

Fig. 4 Eggshell microstructure of *Parafaveoloolithus microporus* oosp. nov., V 16857.1

A, A'. 径切面,箭头示蛋壳内部生长出的锥体 radial view, note cone developing within eggshell (arrow), A. 线条图 line drawing, A'. 照片 photo; B. 近外表面处弦切面 tangential view near outer surface of eggshell; C. 蛋壳中部弦切面 tangential view in middle part of eggshell; D. 近内表面处弦切面 tangential view near inner surface of eggshell; 比例尺 scale bars = 300 μm

略有扩大。在近内表面处所有的气孔道相互连通,气孔道壁被分割成由不规则壳单元组成的块状体(图 4D)。

比较与讨论 该种蛋化石外形类似宁夏蜂窝蛋,但略大一些;径切面上气孔道直而少分枝,也与宁夏蜂窝蛋的情况相似。但是它的壳单元为细长的柱状,无生长纹,锥体细小且放射状结构不发育,壳单元重叠生长的层次较少;另外,在近内表面的弦切面上,气孔道壁分割成独立的块状体。由此可见,虽然在外形、大小和蛋壳径切面的总体特征上接近宁夏蜂窝蛋,但该种蛋化石壳单元的形态和排列方式与宁夏蜂窝蛋明显不同,所以它仍然被归入蜂窝蛋科,并且代表该科的一个新蛋属——副蜂窝蛋属。

值得一提的是,在蒙古北戈壁 Ologoy-Ulan-Tsav 高地发现的具"多孔蛋壳"的蛋化石曾被 Mikhailov 等(1994)鉴定为宁夏蜂窝蛋,然而其蛋壳厚度及径切面显微结构等方面的特征更接近于本文描述的副蜂窝蛋。尤其是 Sochava (1969)描述的蛋化石(No 2970/1),形态接近球形,壳厚为 1.8 ~2.5 mm, 蛋壳径切面上壳单元为细长的柱状,在近内表面的弦切面上气孔道壁也被分割成不规则的块状体。另有一些蛋化石在正交偏光下同样可见长柱状的壳单元及其中细小的锥体(Sochava, 1971)。根据以上这些特点,蒙古的这些蛋

化石可以被归入副蜂窝蛋属。另外,方晓思等(1998)描述的杨氏蛋属新蛋种——西坪杨氏蛋(*Youngoolithus xipingensis*), 其形态为扁圆形,壳厚 1.7 ~ 2.0 mm。蛋壳径切面上壳单元窄长,气孔道直而少分枝,从总体特征上看也应归于副蜂窝蛋属。不过这枚蛋化石明显更大,形态上更接近椭圆(长径 170 mm,最大横径 143 mm,形态指数 84.1),有可能代表一个新蛋种。

大孔副蜂窝蛋(新蛋种) *Parafaveoloolithus macroporus* oosp. nov.

(图 5,6)

词源　种名 *macroporus* 意为"大孔隙的",表明该种蛋化石气孔直径特别大。

正型标本　13 块碎蛋壳,采自一窝大约 4 枚蛋中的 3 枚,野外地点编号 T071201-D1,标本编号 IVPP V 16858。

地点和层位　浙江省天台县赖家村北方山脚下,赖家组红色泥岩中,上白垩统。

特征　蛋化石椭圆形,蛋壳通常由一层长柱状壳单元组成,少数部位由两个壳单元重叠而成,锥体较发达,呈锥状。气孔道较粗。

描述　这窝蛋发现于赖家村北通往方山的一条小路边,仅有部分蛋化石暴露在外。比较清楚的有 4 枚,椭圆形,可以辨认出尖端和钝端,但两端区别不太明显(图 5)。从这几枚蛋化石来看,它们基本位于同一平面上,其长轴大致有共同的走向,但并不相互平行。保存较好的两枚蛋化石的长径分别为 135 和 130 mm, 最大横径都为 100 mm, 形态指数分别为 74 和 76。

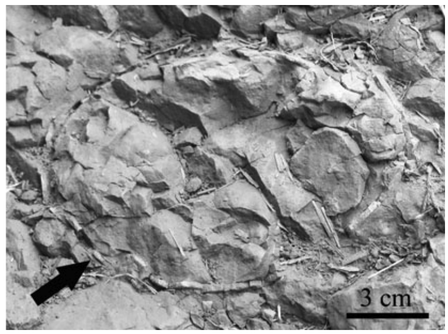

图 5　大孔副蜂窝蛋(新蛋种),V 16858,箭头示一枚风化了的蛋化石

Fig. 5　*Parafaveoloolithus macroporus* oosp. nov., V 16858, arrow indicates a weathered egg

蛋壳外表面光滑,厚度为 1.85 ~ 1.90 mm。径切面上气孔道直,极少分枝。有的气孔道宽度很稳定,有的则向外表面逐渐变窄。气孔道壁通常由一层长柱状壳单元组成,少数部位由两个较短的壳单元叠覆而成,壳单元内棱柱体之间界线分明。近内表面处可见锥体呈锥形,放射状结构很发育(图 6A, A')。

从弦切面上看,蛋壳结构为蜂窝状。近外表面处气孔近圆形,直径较小(图 6B)。蛋壳中部气孔以形态不规则者居多,密度为 12 个/mm^2; 气孔直径增大,变异范围为 0.04 ~ 0.64 mm, 平均 0.27 mm (图 6C)。近内表面处气孔大多相互连通,气孔道壁被分隔成块状,由具放射状结构的不规则壳单元组成(图 6D)。

比较与讨论　从蛋壳的显微结构上看,该蛋化石与 *P. microporus* 比较相似:1) 气孔道都比较直且很少分枝;2) 壳单元都为细长的柱状且棱柱体间界线清晰;3) 叠覆生长的壳单元在这两种蛋中都比较少见。因此将这个标本也归入副蜂窝蛋属。不过,它们之间仍有一些区别:这里描述的蛋化石更接近椭圆形,蛋壳稍薄;锥体呈锥形,相对比较发达;气孔道直径明显较大,气孔密度显著较小。从以上几个方面来看,虽然出土的层位接近,但它们无疑是两个不同的蛋种。

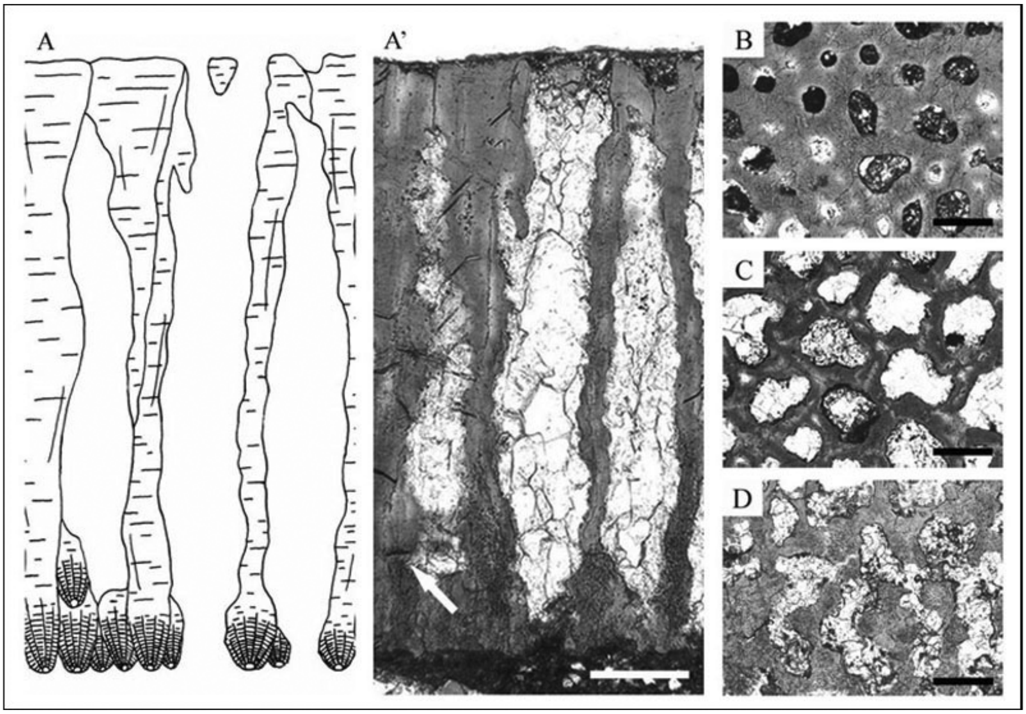

图 6 大孔副蜂窝蛋(新蛋种)蛋壳显微结构,V 16858

Fig. 6 Eggshell microstructure of *Parafaveoloolithus macroporus* oosp. nov., V 16858

A, A'. 径切面,箭头示蛋壳内部生长出的锥体 radial view, note cone developing within eggshell (arrow), A. 线条图 line drawing, A'. 照片 photo; B. 近外表面处弦切面 tangential view near outer surface of eggshell; C. 蛋壳中部弦切面 tangential view in middle part of eggshell; D. 近内表面处弦切面 tangential view near inner surface of eggshell; 比例尺 scale bars = 300 μm

田思村副蜂窝蛋(新蛋种) *Parafaveoloolithus tiansicunensis* oosp. nov.

(图 7)

词源 种名中 tiansicun 为化石产地的汉语拼音。

正型标本 11 块碎蛋壳及嵌在一块岩石中的一些蛋壳,野外地点编号 T080526-D13, 标本编号 IVPP V 16859。

地点和层位 浙江省天台县田思村,上白垩统赤城山组。

特征 蛋壳通常由一层柱状壳单元组成,少数部位由 2–3 个壳单元重叠生长而成。锥体较粗大,为柱状。气孔道下部较膨大,在近外表面处明显变窄。

描述 蛋壳外表面光滑,厚度为 1.37 ~ 1.45 mm。气孔道直,几乎不见分枝,下部或中部常稍微膨大,接近蛋壳外表面处则明显变窄,在蛋壳外表面上仅有很小的开口。蛋壳内通常只能见到一层壳单元,少数部位由 2–3 个壳单元重叠生长而成。壳单元柱形或略呈锥形,棱柱体之间的界线十分清晰。内表面处锥体膨大为柱状,放射状结构发育(图 7A, A')。

在蛋壳近外表面的弦切面上,气孔为细小的圆孔,或稍大一些的不规则孔洞(图 7B)。向内表面方向气孔直径迅速增大,蛋壳结构呈现蜂窝状。在蛋壳中部的弦切面上,气孔多

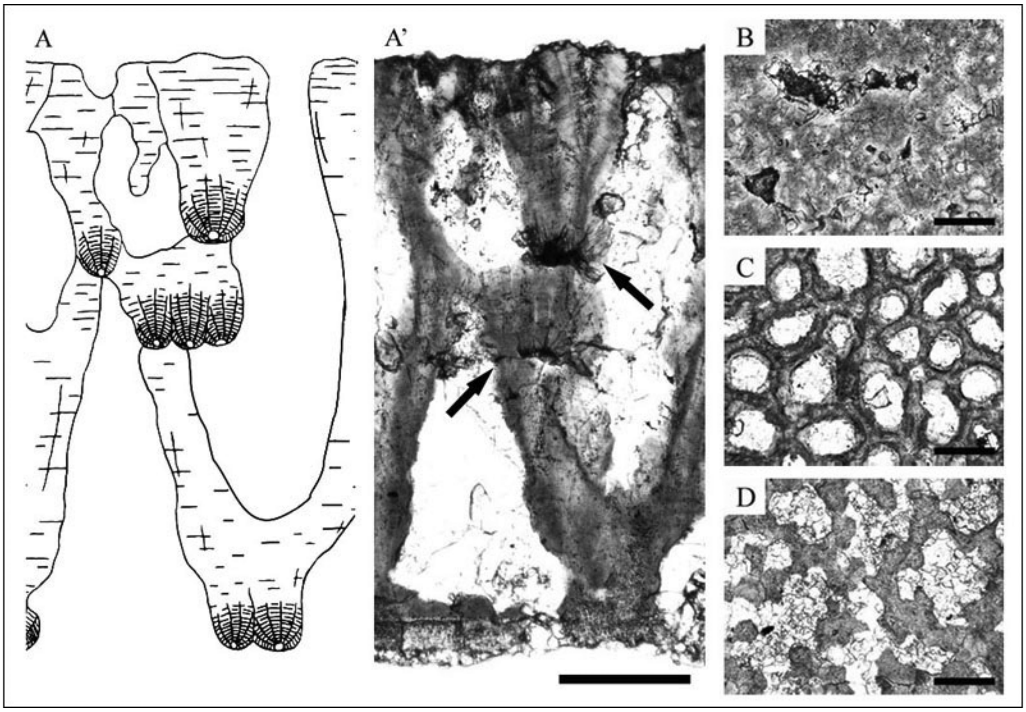

图 7　田思村副蜂窝蛋(新蛋种)蛋壳显微结构,V 16859

Fig. 7　Eggshell microstructure of *Parafaveoloolithus tiansicunensis* oosp. nov., V 16859

A, A'. 径切面,箭头示叠覆生长的壳单元 radial view, note superimposed shell units (arrows), A. 线条图 line drawing, A'. 照片 photo; B. 近外表面处弦切面 tangential view near outer surface of eggshell; C. 蛋壳中部弦切面 tangential view in middle part of eggshell; D. 近内表面处弦切面 tangential view near inner surface of eggshell; 比例尺 scale bars = 300 μm

数近圆形或略拉长(图 7C), 直径变异范围为 0.10 ~0.42 mm, 平均 0.21 mm, 密度为 17 个/mm^2。近内表面处气孔相互连通,气孔道壁被分割成由不规则壳单元组成的块体(图 7D)。

比较与讨论　这里描述的蛋壳通常由一层柱状壳单元组成,棱柱体间界线清晰,可将其归入副蜂窝蛋属。但其蛋壳中部的气孔直径和密度介于 *P. microporus* 和 *P. macroporus* 之间;锥体为柱形,可区别于 *P. microporus* 不发达的锥体和 *P. macroporus* 锥形的锥体;蛋壳厚度比 *P. microporus* 和 *P. macroporus* 都薄;近外表面处气孔道明显变窄这一特征也不见于前述的这两种副蜂窝蛋。所以它应当是一个新蛋种。

杨氏蛋科(新蛋科) Youngoolithidae oofam. nov.

鉴别特征　见杨氏蛋属的模式蛋种夏馆杨氏蛋的修订特征。

杨氏蛋属 *Youngoolithus* Zhao, 1979

修订属征　见模式蛋种夏馆杨氏蛋的修订特征。

夏馆杨氏蛋 *Youngoolithus xiaguanensis* Zhao, 1979

(图 8,9)

正型标本　一窝共 16 枚蛋。野外地点编号 75029, 标本编号 IVPP V 5783。

地点和层位　河南省内乡县夏馆后庄北东 0.5 km 处的紫红、棕红色砂质泥岩夹薄层灰白色砂砾岩中,白垩系(赵资奎,1979a)。

修订特征　蛋化石橄榄形,长轴指向同一方向并前后交错地成排排列。蛋壳总体为蜂窝状结构,常由 2-4 个壳单元重叠生长而成。壳单元为较短小的柱状,生长纹不发育,排列方式很不规则,在近内表面处相互分离。气孔道多数分枝且较弯曲。

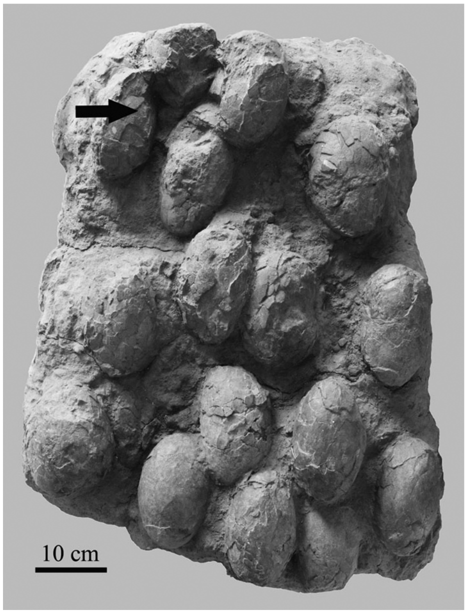

图 8　夏馆杨氏蛋,V 5783
箭头所示处为一个恐龙脚印
Fig. 8　*Youngoolithus xiaguanensis*, V 5783
Arrow indicates a dinosaur footprint

描述　蛋化石似橄榄形,近乎两端对称,有一些可以分辨出尖端和钝端(图 8)。蛋化石长径 156.0 ~173.4 mm, 平均 165.6 mm; 最大横径 91.0 ~109.4 mm, 平均 98.9 mm; 形态指数为 53.7 ~66.8, 平均 59.8。

蛋化石在窝中大致排列在同一平面上,长轴方向相同。从平面上看,它们大致能分成 5 排,每排 3-4 枚,相邻的两排之间前后交错排列。由于蛋窝一端有两枚不完整的蛋化石,所以这不是一个完整的蛋窝(图 8)。

蛋壳厚度为 1.45 ~1.60 mm, 平均 1.56 mm, 外表面很光滑。从径切面上看,蛋壳中均匀分布着贯通整个蛋壳的气孔道。这些气孔道弯曲且分枝较多,同一条气孔道的直径变化比较大,并且在近外表面处略有变窄。蛋壳通常由 2-4 个壳单元重叠生长而成,近外表面处常有较短小的壳单元成层生长。从整体上看,壳单元的排列方式很不规则,因此蛋壳径切面的结构与网形蛋类有些相似。单个的壳单元呈短小的柱状,锥体细小,棱柱体之间界线清晰,无生长纹(图 9A, A')。

从弦切面上看,蛋壳总体结构为蜂窝状,气孔大多数近圆形。蛋壳中部气孔直径的变异范围为 0.07 ~0.33 mm, 平均值为 0.17 mm, 气孔密度为 26 个/mm^2(图 9C), 近外表面处气孔的直径和密度均较蛋壳中部的小(图 9B)。向内表面方向不规则的气孔增加,相邻的气孔多半相互连通。近内表面处气孔道壁被分割成独立的块状体,每个块状体都由几个具有放射状结构的块状壳单元侧向融合而成(图 9D)。

比较与讨论　与蜂窝蛋科的成员相比,夏馆杨氏蛋有许多重要的不同点。首先,最直观的是宏观形态和蛋窝结构上的区别:夏馆杨氏蛋为橄榄形,在蛋窝中长轴相互平行且前后交错排列;蜂窝蛋科的成员为近圆形或椭圆形,并且以宁夏蜂窝蛋为代表,它们在蛋窝中是无规则排列。所以可认为,夏馆杨氏蛋与蜂窝蛋科的蛋化石是由亲缘关系比较远的

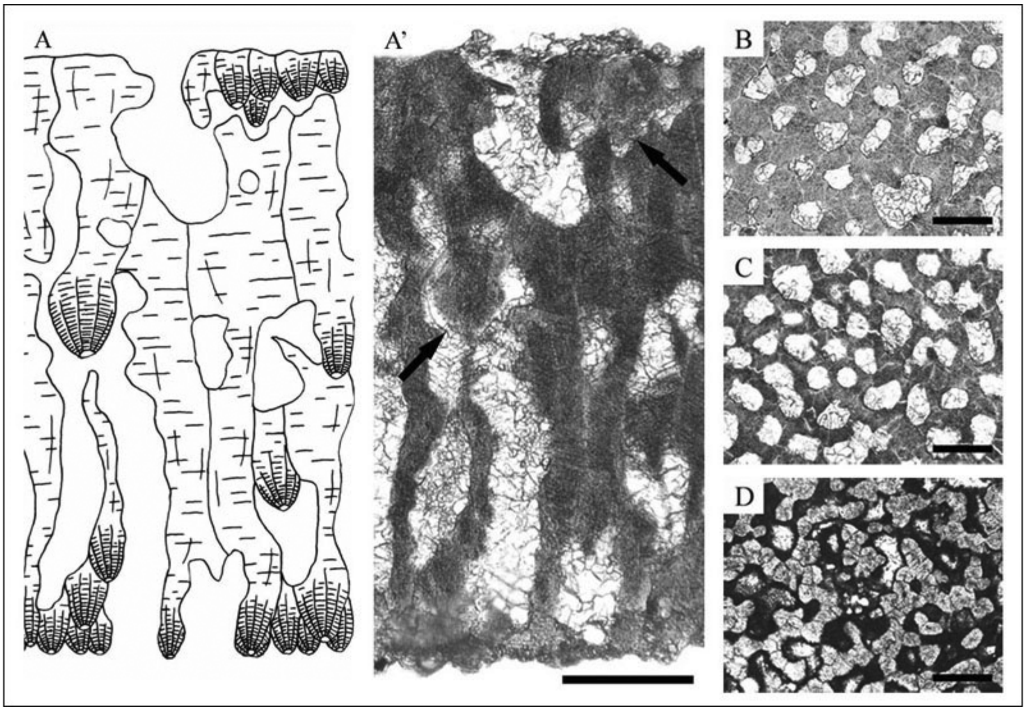

图 9　夏馆杨氏蛋蛋壳显微结构, V 5783

Fig. 9　Eggshell microstructure of *Youngoolithus xiaguanensis*, V 5783

A, A'. 径切面,箭头示叠覆生长的壳单元 radial view, note superimposed shell units (arrows), A. 线条图 line drawing, A'. 照片 photo; B. 近外表面处弦切面 tangential view near outer surface of eggshell; C. 蛋壳中部弦切面 tangential view in middle part of eggshell; D. 近内表面处弦切面 tangential view near inner surface of eggshell; 比例尺 scale bars = 300 μm

两类恐龙产的。其次,夏馆杨氏蛋的气孔道较曲折且多分枝,壳单元较短小,叠覆生长的层次较多,排列方式很不规则;蜂窝蛋科的成员气孔道较直且少有分枝,壳单元较长,叠覆生长的层次较少,排列得相对规整一些。通过以上的比较,可以根据夏馆杨氏蛋的特征建立一个新蛋科——杨氏蛋科。那么,由杨氏蛋科和蜂窝蛋科代表的具有蜂窝状蛋壳组织结构的恐龙蛋可以构成高于科一级的分类单元。

3　蜂窝蛋的分类特征及鉴定方法

宁夏蜂窝蛋和夏馆杨氏蛋在最初研究的时候根据其宏观形态、在蛋窝中的排列方式和蛋壳显微结构特征被置于两个不同的蛋属中。然而,在浙江天台新发现的三种蜂窝蛋在宏观形态和蛋壳显微结构上与宁夏蜂窝蛋比较接近,而与夏馆杨氏蛋差异较大,所以将它们与宁夏蜂窝蛋的差异视为属一级的区别,夏馆杨氏蛋与宁夏蜂窝蛋的差异则相应地为科一级区别。由此可见,依据蛋化石宏观形态、在蛋窝中的排列方式和蛋壳显微结构的总体特征可区分较高级的,如科一级的分类单元。属一级的分类单元可通过壳单元的形

态及其排列方式区分。如宁夏蜂窝蛋的壳单元为粗大的锥形,重叠生长的层次相对较多,因而与产自浙江天台的蛋壳通常由一层柱状壳单元组成的蜂窝蛋划归为不同的蛋属。种一级的区分则根据蛋壳的厚度、壳单元形态上的细节差异和气孔的直径及密度这几个特征,其中气孔直径和密度是主要的划分依据。

为了观察到以上鉴定特征,从而判断一枚蛋化石是否为蜂窝蛋,并给它一个合适的分类位置,应当按照如下的步骤进行鉴定:

首先,一枚蛋化石如果从蛋壳径切面上看有可能是蜂窝蛋的话,则须制作弦切面组织切片以确认其具有蜂窝状的组织结构,从而排除是网形蛋的可能;之后再通过蛋化石宏观形态、蛋壳径切面结构的总体特征和蛋窝结构判断它所属的蛋科;最后根据上述蛋属、蛋种的鉴定特征确定其分类位置。需要强调的是,在测量气孔直径和密度时要特别注意尽量选取蛋壳中部的弦切面进行测量。这是因为蜂窝蛋气孔的直径和密度至蛋壳中部处已相对稳定,气孔形态也相对比较规则,便于测量。同时,选取固定的位置进行测量,也使不同种蛋化石的数据之间有较好的可比性。不过,如果蛋壳中部的气孔形态大多不规则(如 *P. macroporus*),则尽可能选取形态相对规则者,并测其最大的直径。

致谢 在野外工作期间,汪筱林、赵资奎研究员、博士生王强和技术室高伟、李岩,以及浙江省天台县国土资源局蒋严根高级工程师给予全力帮助和指导。在论文的写作中,得到导师赵资奎研究员的悉心指导,汪筱林研究员审阅初稿并提出许多修改意见,王强协助实验室切片并提出一些建设性意见,Corwin S. Sullivan 博士帮助修改英文部分,沈文龙协助绘制插图。在此向他们表示衷心的感谢。

A PARATAXONOMIC REVISION OF THE CRETACEOUS FAVEOLOOLITHID EGGS OF CHINA

ZHANG Shu-Kang

(1 *Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044 zskcamp. student@ sina. com)

(2 *Graduate University of Chinese Academy of Sciences* Beijing 100049)

Key words Tiantai Basin, Zhejiang; Late Cretaceous; faveoloolithid egg; taxonomy

Summary

The Faveoloolithidae, erected by Zhao and Ding (1976), were first described from the Albian-Cenomanian of the Gobi Desert, Mongolia (Sochava, 1969, 1971), and were assigned the name multicanaliculate. The group includes *Faveoloolithus ningxiaensis* Zhao & Ding, 1976 from the Cretaceous of Alxa, Nei Mongol and *Youngoolithus xiaguanensis* Zhao, 1979 from the Cretaceous of Xiaguan Basin, Henan Province. So far, faveoloolithid eggs have been reported from Xichuan, Xixia (Zhou and Han, 1993; Zhang and Li, 1998) and Wulichuan basins (Zhou and Feng, 2002) in Henan Province, Jinqu, Tiantai (Zhang and Li, 1998) and Yongkang basins (Yu et al., 2003) in Zhejiang Province, and Qinglong Mountain in Hubei Province (Guan et al., 1997; Zhou et al., 1998). Clutches have also been found in Khermiyn-Tsav and Ikh-Shunkht in Mongolia (Mikhailov et al., 1994), and Bosung in South Korea (Huh and Zelenitsky, 2002). However, except for *F. ningxiaensis* and *Y. xiaguanensis*, other specimens'

parataxonomic position within Faveoloolithidae was uncertain.

In this paper, detailed redescriptions of the holotypes of *F. ningxiaensis* and *Y. xiaguanensis*, and of some new material from Tiantai Basin, Zhejiang Province, are presented along with comments on the parataxonomy of this group of eggs.

Faveoloolithidae Zhao & Ding, 1976

Revised diagnosis Eggs spheroidal or oval, with smooth outer surface and honeycomb-like eggshell structure. Eggshell composed of one layer of shell units or 2-3 superimposed shell units. Pore canals more or less straight.

Faveoloolithus Zhao & Ding, 1976

Revised diagnosis See the revised diagnosis of the type oospecies *Faveoloolithus ningxiaensis*.

Faveoloolithus ningxiaensis Zhao & Ding, 1976

(Figs. 1,2)

Holotype A nest containing 11 eggs (IVPP V 4709; Field No. 73032).

Referred specimen A broken egg (IVPP V 16856; Field No. S202).

Locality and horizon Chahanaobao, Bayinwula Mountain, Alxa Left Banner, Nei Mongol; red to purple conglomeratic grit on the banks of a gully, Cretaceous (Zhao and Ding, 1976).

Revised diagnosis Eggs spheroidal, arranged irregularly in nest. Eggshell composed of 2-3 superimposed shell units. Shell units cone-shaped with well-developed growth lines, not separated near inner surface of eggshell.

Description The eggs are arranged irregularly in the nest. The space between adjacent eggs is about 10 ~ 40 cm. One incomplete egg is directly superimposed on another egg, indicating that there may have been more than one layer of eggs initially (Fig. 1).

The eggs are 130.8 ~ 143.7 mm long and 117.6 ~ 127.9 mm wide, the average length and width being 133.6 mm and 120.3 mm respectively. The average shape index is 92.7, indicating a spheroidal shape.

The outer surface of each egg is smooth. The eggshell is 1.20 ~ 1.54 mm thick, with an average of 1.40 mm. Radial views reveal that the eggshell usually consists of 2-3 superimposed shell units. The radial texture and growth lines of each shell unit are well-developed. The pore canals are more or less straight (Fig. 2A, A').

Tangential views show that most of the pores are round, with a smaller diameter near the outer surface (Fig. 2B). In the middle part of the eggshell, the pore diameter is 0.07 ~ 0.40 mm, with an average of 0.20 mm. The pore density is 18 per mm^2. The number of irregular pores increases towards the inner surface of the eggshell, where the pores are quite irregular in shape but have complete walls (Fig. 2C, D).

Discussion When Zhao and Ding (1976) studied this specimen, they were unable to observe the shell units because of the limited equipment available, and regarded the eggshell as a uniform calcite layer. According to my observations, the eggshell of *F. ningxiaensis* is composed of many superimposed shell units. New shell units are deposited on top of primary ones and all the shell units fuse together transversely, forming a honeycomb-like structure. Thus, it can be seen that the eggshell formation pattern of *F. ningxiaensis* is totally different from that seen in dinosaur eggs with an avian-like eggshell structure.

Parafaveoloolithus oogen. nov.

Etymology Para-, from Greek *para*, means "beside, near"; -faveoloolithus, from the oogenus name of *Faveoloolithus ningxiaensis*.

Type oospecies *Parafaveoloolithus microporus* oosp. nov.

Diagnosis Eggs spherical or oval. Eggshell composed of one layer of shell units, or two superimposed shell units in some portions. Shell units incomplete and prismatic, separated from each other near inner surface of eggshell. Growth lines undeveloped within shell units; boundaries between prisms relatively clear.

Parafaveoloolithus microporus oosp. nov.

(Figs. 3, 4)

Etymology The oospecies name means small pore, referring to the narrowness of the pore canals.

Holotype A crushed incomplete egg (IVPP V 16857.1; Field No. 45).

Referred specimen Another incomplete egg (IVPP V 16857.2; Field No. 45).

Locality and horizon Fangshan, Tiantai County, Zhejiang Province; Laijia Formation, Upper Cretaceous.

Diagnosis Egg spherical. Eggshell usually composed of one layer of slender prismatic shell units, or two superimposed shell units in some portions. Cones tiny. Pore canals narrow and closely spaced.

Description V 16857.1 is 141.06 mm long and 129.44 mm wide, with a shape index of 91.8; V 16857.2 is 149.12 mm long (Fig. 3). The eggshell thickness varies between 2.20 and 2.35 mm. Radial views show that the eggshells are usually composed of one layer of shell units, or two superimposed shell units in some portions. The cones are tiny, with undeveloped growth lines. The pore canals are straight and unbranching, extremely numerous, and closely spaced (Fig. 4A, A'). In tangential sections through the middle part of the eggshell, the pore diameter varies between 0.06 and 0.25 mm, with an average of 0.15 mm. Pore density is 35 per mm^2. Most of the pores are round, but some are irregular (Fig. 4B, C). Near the inner surface, all the pores connect to each other; the pore walls are separated into small blocks composed of irregular shell units (Fig. 4D).

Comparison and discussion The specimens described above are similar to *F. ningxiaensis* eggs in general external shape and pore canal morphology, but are slightly bigger. Accordingly, both of them belong to Faveoloolithidae. However, based on the slender prismatic shell units, the tiny cones, the rarity of superimposition among the shell units and the separation of shell units near the inner surface of the eggshell, these eggs are referred to a new faveoloolithid oogenus, *Parafaveoloolithus*.

In addition, the "multicanaliculate" eggs discovered in Ologoy-Ulan-Tsav in the northern Gobi (Sochava 1969, 1971) and identified as *F. ningxiaensis* by Mikhailov et al. (1994), and the oospecies *Youngoolithus xipingensis* described by Fang et al. (1998), should be assigned to this new oogenus based on their slender prismatic shell units and straight pore canals.

Parafaveoloolithus macroporus oosp. nov.

(Figs. 5, 6)

Etymology The oospecies name *macroporus* means "big pore", indicating that the diameter of the pores within the eggshell is large.

Holotype 13 eggshell fragments (IVPP V 16858; Field No. T071201-D1), belonging to three eggs in the same nest.

Locality and horizon Laijia Village, Tiantai County, Zhejiang Province; Laijia Formation, Upper Cretaceous.

Diagnosis Eggs oval, with unbranching large straight pore canals. Eggshell composed of one layer of slender prismatic shell units, or occasionally two superimposed shorter shell units. Cones clear, with well-developed radial texture.

Description The eggs are oval and nearly symmetrical (Fig. 5). The long axes of these eggs are approximately in the same direction, but not parallel. The lengths of two well-preserved eggs are 135 mm and 130 mm; both eggs are 100 mm wide, and their respective shape indices are 74 and 76.

Eggshell thickness is 1.85 ~ 1.90 mm. Radial views show that the pore canals are straight and unbranching, and that some of them narrow gradually near the outer surface of the eggshell. The pore canal walls are usually composed of one layer of slender prismatic shell units, or two superimposed shorter shell units in some portions. The boundaries between prisms are clear. The cones near the inner surface of the eggshell are cuspate, with a well-developed radial texture (Fig. 6A, A').

In tangential sections, the pores appear round and relatively small near the outer surface of the eggshell (Fig. 6B). In the middle part of the eggshell, most of the pores are irregular. Their diameters in this region range from 0.04 mm to 0.64 mm, with the average being 0.27 mm. Pore density is 12 per mm^2 (Fig. 6C). All the pores connect to each other, and the pore walls become separated into small blocks, near the inner surface of the eggshell (Fig. 6D).

Comparison and discussion The microstructure of the eggshell in this oospecies is similar to that seen in *P. microporus*: 1) pore canals are straight and unbranching; 2) shell units are slender and prismatic, with clear boundaries between prisms; and 3) the cones are rare within the substance of the eggshell. Considering these characters, these eggs are assigned to the oogenus *Parafaveoloolithus*. Nevertheless, the differences between these specimens and *P. microporus* eggs are remarkable. The eggs described here are more elongated than *P. microporus*, and have slightly thinner shells. Furthermore, the pores of the specimens described here are much bigger, and the pore density in the middle part of the eggshell is much lower. Accordingly, these eggs are regarded as belonging to an oospecies distinct from *P. microporus*.

Parafaveoloolithus tiansicunensis **oosp. nov.**

(Fig. 7)

Etymology From "Tiansicun" (Tiansi Village), the name of the locality where the specimens were collected.

Holotype 11 eggshell fragments and some eggshells embedded in rock (IVPP V 16859; Field No. T080526-D13).

Locality and horizon Tiansi Village, Tiantai County, Zhejiang Province; Chichengshan Formation, Upper Cretaceous.

Diagnosis Eggshells usually composed of one layer of prismatic shell units, or 2–3 superimposed shell units in some portions. Cones large and columnar, showing well-developed radial texture near inner surface of eggshell. Unbranching straight pore canals expanded in inner part of eggshell, narrowing sharply near outer surface.

Description Eggshell thickness in this oospecies varies between 1.37 and 1.45 mm. The pore canals are straight, and narrow sharply near the outer surface of the eggshell. The openings on the outer surface are very small. Generally, the eggshell is composed of one layer of prismatic shell units, but there are 2–3 relatively shorter shell units superimposed on each other in some portions. The shell units are prismatic or cone-shaped. The boundaries between prisms are very clear. There are swollen cones near the inner surface of the eggshell (Fig. 7A, A').

In tangential sections taken near the outer surface of the eggshell, the pores appear round or irregular (Fig. 7B). Pore diameter increases towards the inner surface of the eggshell. The pores are round or oval in the middle part of the eggshell (Fig. 7C), with diameters ranging from 0.1 mm to 0.42 mm and averaging 0.21 mm. Pore density is 17 per mm^2. The pores connect to each other near the inner surface of the eggshell, and the pore walls become separated into small blocks formed from irregular shell units (Fig. 7D).

Comparison and discussion These specimens should be assigned to *Parafaveoloolithus* on the basis of their prismatic shell units, the clear boundaries between prisms, and the rarity of superimposed shell units. However, pore diameter and pore density are intermediate between *P. microporus* and *P. macroporus*; the cones are columnar, differing from both the undeveloped cones of *P. microporus* and the cuspate cones of *P. macroporus*; the eggshell is thinner than in the other specimens from Tiantai Basin; and the sharp narrowing of the pore canals near the outer surface of the eggshell is unique. In sum, the specimens described here represent a new oospecies.

Youngoolithidae oofam. nov.

Diagnosis See the revised diagnosis of the type oospecies of *Youngoolithus*, *Y. xiaguanensis*.

Youngoolithus Zhao, 1979

Revised diagnosis See the revised diagnosis of the type oospecies, *Y. xiaguanensis*.

Youngoolithus xiaguanensis Zhao, 1979

(Figs. 8, 9)

Holotype A nest of 16 eggs (IVPP V 5783; Field No. 75029).

Locality and horizon 0.5 km northeast of Houzhuang Village, Xiaguan Town, Neixiang County, Henan Province; purplish red and brown sandy mudstone interbedded with thin layers of gray sandy conglomerate, Cretaceous (Zhao, 1979a).

Revised diagnosis Eggs olive-shaped, arranged in rows. Eggshell typically composed of 2–4 superimposed prismatic shell units. Growth lines undeveloped. Most pore canals curved and branched. Pore walls separated into small blocks near inner surface of eggshell.

Description The eggs are olive-shaped and nearly symmetric. The eggs are 156.0 ~ 173.4 mm long and 91.0 ~ 109.4 mm wide, with the length and width averaging 165.6 mm and 98.9 mm respectively. The shape index varies between 53.7 and 66.8, with an average of 59.8. The eggs are arranged in five rows, with 3–4 eggs in each row. The long axes of these eggs are in the same direction. Adjacent rows interlace with one another (Fig. 8).

Eggshell thickness is 1.45 ~ 1.60 mm, with an average of 1.56 mm. The outer surface of each eggshell is smooth. In radial section, the crooked pore canals can be seen to have many branches and to be highly variable in diameter, narrowing slightly near the outer surface of the eggshell. The eggshells are usually composed of 2–4 superimposed prismatic shell units. In some portions, very short shell units are arranged in a single layer beneath the outer surface of the eggshell. Therefore, the eggshell structure is rather irregular in radial section, resembling the reticular eggshell structure of dictyoolithid eggs. The shell units are characterized by tiny cones, undeveloped growth lines and visible boundaries between prisms (Fig. 9A, A').

Most of the pores are round in tangential section. In the middle part of the eggshell, pore diameter ranges from 0.07 mm to 0.33 mm, with a mean value of 0.17 mm. Pore density is 26 per mm^2 (Fig. 9C). Near the outer surface, pore diameter and density are slightly smaller (Fig. 9B). The number of irregular pores increases towards the inner surface of the eggshell, where all the pores connect to each other and the pore walls are separated into small blocks (Fig. 9D).

Comparison and discussion Compared to the members of Faveoloolithidae, *Y. xiaguanensis* has following differences. The most remarkable differences lie in the macromorphological characters of the eggs and the nest. As demonstrated by *F. ningxiaensis*, faveoloolithid eggs are spherical and arranged irregularly in the nest. However, *Y. xiaguanensis* eggs are olive-shaped and arranged in rows. Based on this comparison, it is reasonable to assume that

Y. xiaguanensis and faveoloolithid eggs belong to dinosaurs that are only distantly related. Second, in contrast to the branching pore canals and the relatively shorter and irregularly arranged shell units of *Y. xiaguanensis*, the pore canals of faveoloolithid eggs are straight and their shell units are more regularly arranged. Consequently, *Y. xiaguanensis* should be assigned to a new oofamily, Youngoolithidae. Furthermore, it is safe to say that dinosaur eggs with a honeycomb-like eggshell structure form a taxon above the family level.

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