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伤齿龙(Troodontids)筑巢产卵的行为

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摘要　应用薄壳理论研究中国和北美西部出土的晚侏罗世至晚白垩世伤齿龙蛋以平卧和竖立两种方式埋在沙土中受压破损的抵抗能力,分析伤齿龙蛋在蛋窝中特有的排列方式与其蛋壳的抗失稳能力之间的关系。结果表明,由于伤齿龙蛋壳很薄,其抗失稳能力很差,如果这种蛋以横卧方式埋在沙土中就可能在很小载荷下因失稳屈曲而破裂;但是,如果把蛋竖立起来埋在沙土中,则蛋的抗破碎能力比把它们平放埋在沙土中要高出4～5倍。从而认为,伤齿龙在筑巢产卵时把一个个蛋竖立起来埋在沙土中是为解决其低强度蛋壳在保护胚胎,避免外力损伤和在卵的孵化后期幼雏能够破壳而出这两方面的矛盾而采取的一种保护性措施,说明这些体征很像鸟类的兽脚类恐龙,其智商可能比人们想象的要高。在此基础上,探讨和复原了伤齿龙筑巢产卵的行为。

关键词　伤齿龙蛋,临界载荷,临界应力,失稳,破碎强度,筑巢行为

中图法分类号　Q915.21

恐龙的繁殖行为一直是人们很感兴趣的一个问题。很早就有人推测恐龙的繁殖行为应和现生爬行动物的相似,但这只是根据生物学上生态特征的一致性原则来推测的。由于恐龙早在6 500万年前就已灭绝,它们在世界上的一切活动都已成了历史的事件,我们只能通过它们遗留在地层里的化石来了解恐龙。

伤齿龙蛋在蛋窝中的排列方式非常奇特。每个蛋都是垂直或稍微倾斜地竖立在蛋窝中(Horner,1984,图5;赵资奎、李荣,1993,图版Ⅰ;Zhao,2000,图1),蛋较尖的一端朝下。伤齿龙在筑巢产卵时为什么要这样把一个个蛋竖立起来埋在沙土中?这种筑巢产卵行为是否具有古生物学意义?

赵资奎等(1994)提出,不同类型的恐龙蛋,虽然其形状、大小各不相同,但大体上为旋转对称外形。由于这些蛋的蛋壳厚度远小于轴的长度,也远小于转动半径,从力学的角度上,可以把它看成是一个绕其长轴旋转而成的壳体。当它们被产下埋在沙土中孵化时,就会受到分布压力的作用。当此压力逐渐加大达到临界值 p_{cr}时,在蛋壳的某一部位上将突然出现凹陷,壳也随之破坏。此压力值 p_{cr}称为壳的失稳临界载荷。研究表明,不同类型的恐龙蛋在其蛋窝中有不同的排列方式与其蛋壳的抗失稳能力的大小有很大关系(马和中、赵资奎,1994;赵资奎、马和中,1997)。因此根据蛋壳的生物力学性质,可以为探讨恐龙筑巢产卵行为以及与环境之间的关系提供可靠的依据。本文将以中国和北美地区出土的伤齿龙蛋化石的有关资料,应用生物力学的基础理论和分析方法探讨伤齿龙在繁殖时筑巢产卵的行为及有关的古生物学意义。

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1 伤齿龙蛋化石的发现及其分布

伤齿龙蛋化石是1979年首次在美国蒙大拿州西部上白垩统的Two Medicine组发现的(Horner and Makela, 1979;Horner, 1984;Horner and Gorman, 1988)。当时,根据在这些蛋内所含的胚胎骨化石特征,认为是属于一种小型鸟臀类恐龙——棱齿龙类的,命名为*Orodromeus makelai*(Horner and Weishampel, 1988)。稍后,Hirsch和Quinn(1990)又进一步观察了这些蛋壳的显微结构,发现其主要特征是壳单元呈棱柱状,从而为具有这种结构特征的蛋壳归属于这类“恐龙”提供了依据。

1990年在我国内蒙古自治区乌拉特后旗巴音满都呼上白垩统牙道黑达组发现了一窝较为完整的蛋化石,这些化石蛋在蛋窝中的排列形式及蛋壳的结构特征与上述蒙大拿的标本非常相似。根据赵资奎(1975、1979)提出的恐龙蛋分类方法(Parataxonomy),将其命名为戈壁棱柱形蛋(*Prismatoolithus gebiensis*)(赵资奎、李荣,1993)。从那以后,一般都将那些具有棱柱状结构特征的蛋壳(Prismatoolithids)视为“棱齿龙蛋”。然而,Horner和Weishampel在进一步修理蒙大拿发现的这些化石蛋内的胚胎骨化石时,发现原先把蛋内所含的胚胎骨化石鉴定为棱齿龙是错误的。这些胚胎骨骼应属于一种小型兽脚类恐龙——伤齿龙(*Troodon* cf. *T. formosus*),而不是*Orodromeus makelai*(Horner and Weishampel, 1996)。

到目前为止,棱柱形蛋壳先后在法国南部Languedoc的上白垩统(Vianey-Liaud and Crochet, 1993)、美国科罗拉多的上侏罗统Morrison组(Hirsch,1994)、加拿大西部阿尔伯特上白垩统的Oldman组(Zelenitsky and Hills, 1996)、蒙古上白垩统(Mikhailov, 1994)、中国河南西峡盆地下白垩统(王德有、周世全,1995)和广东省南雄盆地上白垩统坪岭组(Zhao, 2000)等地发现。虽然在这些蛋化石里没发现有胚胎骨骼,但它们在蛋窝中的排列方式与那些含有伤齿龙胚胎的蛋的非常相似,蛋壳组织结构模式也基本一致。因此,这些蛋都被认为是伤齿龙或者与伤齿龙相近的属、种产的。

2 伤齿龙蛋壳的结构特征及其生物力学性质

伤齿龙蛋为长椭圆形,一端较钝,另一端略尖(图1);长径110～150mm,短径48～70mm。蛋壳由纤细、棱柱状壳单元密集排列组成,厚度在0.6～1.0mm之间,是目前已知的恐龙蛋中最薄的一类蛋壳。在那些保存完整的蛋窝中,蛋化石都是垂直或稍微倾斜地竖立在蛋窝中,蛋的尖端朝下(图2～4;Horner,1984,图5;Hirsch and Quinn, 1990,图3d;Zelenitsky and Hills, 1996, 图2a)。从已知的化石记录可以看出,从侏罗纪晚期到白垩纪最晚期,不同属、种的伤齿龙蛋在蛋窝中的排列方式和蛋壳基本结构特征都很相似。说明在这段漫长的地质时期中,蛋壳的结构和功能没有大的变化。

蛋壳主要的功能是保护胚胎,避免外力的损伤,限制蛋内水分的蒸发,保证胚胎发育时呼吸气体的交换以及在孵化后期幼雏能够破壳而出。从力学的角度看,蛋壳结构的力学性质对恐龙蛋的孵化有着很大影响(马和中等,1995),其中比较重要的是蛋壳的强度。如上所述,当它们被产下埋在沙土中孵化时,就会受到分布压力的作用。在这种情况下,

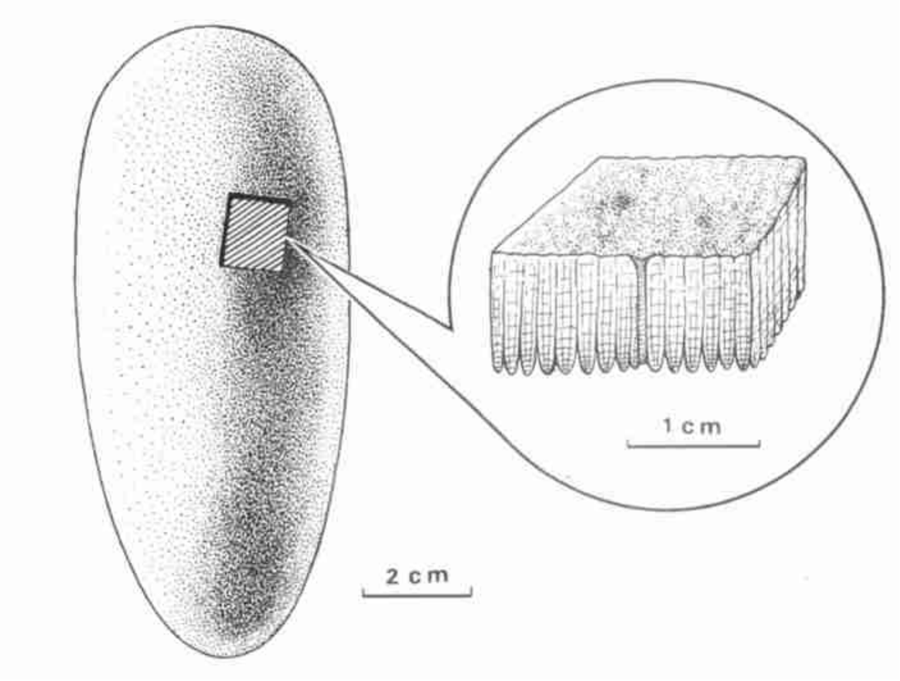

图 1　伤齿龙蛋及其蛋壳结构

Fig. 1　Schematic drawing of troodontid egg and eggshell structure

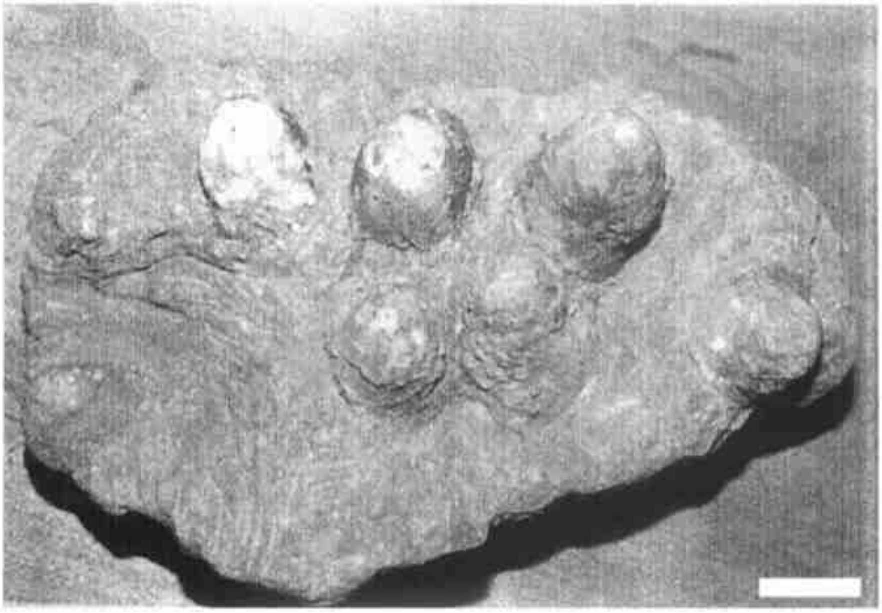

图 2　伤齿龙蛋(*Prismatoolithus* sp.) 一窝,河南省西峡盆地下白垩统

除左右两侧各有一枚蛋化石倾倒外,其余的 5 枚蛋化石都是以直立或稍微倾斜方式埋在蛋窝中

Fig. 2　A clutch of troodontid eggs, *Prismatoolithus* sp., from the Lower Cretaceous rocks of Xixia Basin

The eggs stand vertically, with the exception of the two tipped over on the

right and left side in the clutch, 标尺 scale bar = 5cm

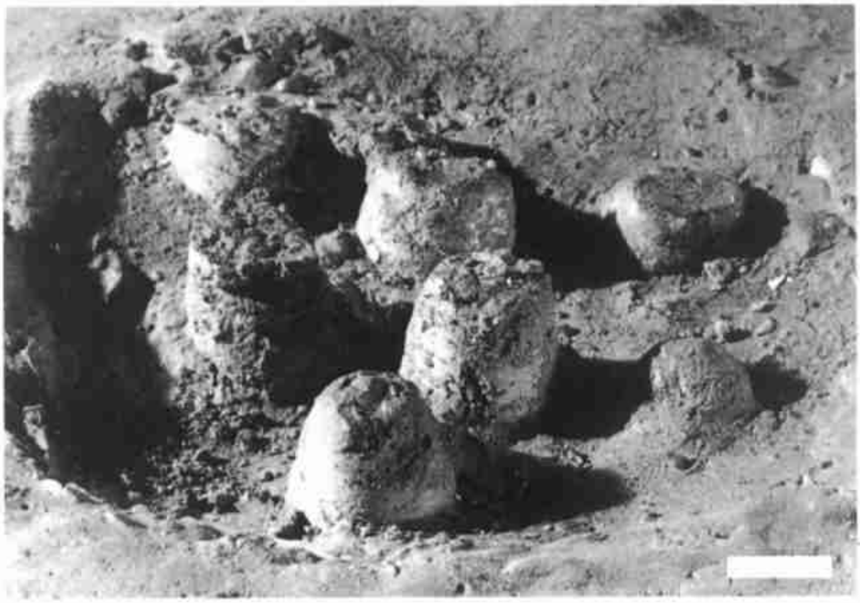

图 3　伤齿龙蛋(*Prismatoolithus gebiensis)* 一窝(NMB 4341) ,内蒙古巴音满都呼上白垩统牙道黑达组 ,蛋化石以直立方式竖立在蛋窝中 ,倒转面观

Fig. 3　A clutch of troodontid eggs , *Prismatoolithus gebiensis* , in the Upper Cretaceous Djadokhta Formation from Bayan Manduhu , Nei Mongol

The clutch with eggs is shown upside down ; eggs stand vertically on their pointed end in nest ; **标尺** scale bar = 5cm

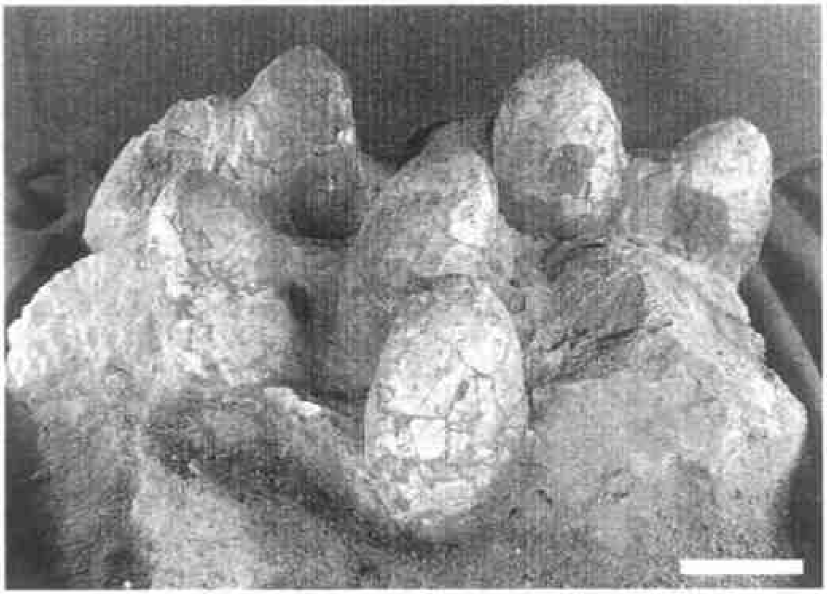

图 4　伤齿龙蛋(*Prismatoolithus hukouensis)* 一窝 ,广东省南雄盆地上白垩统坪岭组 ,倒转面观

Fig. 4　A clutch of troodontid eggs , *Prismatoolithus hukouensis* , in the Upper Cretaceous Pingling Formation from Nanxiong Basin , Guangdong Province , **标尺** scale bar = 5cm

它可能出现两种破坏形式:一种是壳体受压缩破裂;另一种是因压力而失稳(即向内凹陷

屈曲)。如果蛋壳的强度很低,在外压达到失稳临界值 p_{cr}时,在蛋壳的某一部位上将突然出现向内凹陷屈曲而使蛋壳破裂。对鸟蛋壳的试验表明,影响 p_{cr}值的因素主要是蛋壳的几何参数(长轴、半径、厚度等),蛋壳材料的力学性质(弹性模量、泊松比)和外力作用的方向等三个方面。伤齿龙蛋壳已成为化石,它在新鲜情况下的弹性模量和泊松比均不知道。然而伤齿龙蛋壳和鸟蛋壳一样,主要由微晶方解石及少量有机基质组成,蛋壳的基本结构单元及其排列形式也基本相似。因此可以参考鸟蛋壳材料的力学参数,即在同一弹性模量和泊松比的前提下来分析不同时代及不同地区发现的伤齿龙蛋壳的几何形状参数,不同外力作用方向对伤齿龙蛋壳失稳临界分布压力的影响,找出伤齿龙蛋在平卧或竖立的状态下埋在沙土中的抗失稳能力。这样就可以了解伤齿龙在筑巢产卵时把卵竖立起来埋在沙土中的古生物学意义。

法国南部上白垩统发现的伤齿龙蛋(*Prismatoolithus tenuius* 和 *Prismatoolithus matellensis*)由于发现的材料破碎(Vianey-Liaud and Crochet, 1993),而蒙古的标本由于有关的蛋壳各种几何参数不能确定,不适于本文分析,因此本文报告的伤齿龙蛋壳各种几何形状参数主要来源于已发表的中国和北美的材料(表1)。其中 *Prismatoolithus levis* 是根据 Zelenitsky (2000)所提供的数据的平均值;*Prismatoolithus hukouensis* 是作者根据南雄博物馆最近发现的一窝蛋(图3)中一枚完整的化石蛋测量的。

表1　已知的6种伤齿龙蛋化石的几何数据

Table 1　Geometric data of six types of troodontid eggs　(mm)

名　称 Name of the eggs	长　径(L) Long axis	短　径 Diameter	壳　厚 Eggshell thickness	分　布 Distribution	资料来源 References
Prismatoolithus coloradensis	110	60	0.7～1.0	Upper Jurassic of Colorado, USA	Hirsch (1994)
Prismatoolithus sp.	116	48	0.6～0.9	Lower Cretaceous of Xixia Basin, Henan, China	Wang and Zhou (1995); Zhao (2000)
Prismatoolithus gebiensis	120	50	0.7～0.9	Upper Cretaceous (Santonian-Campanian) of Bayan Manduhu, Nei Mongol, China	Zhao and Li (1993)
Prismatoolithus levis	135	65	0.85	Upper Cretaceous (Campanian) of southern Alberta, Canada	Zelenitsky (2000)
Troodon cf. *T. formosus*	150 115 117	66 61 62	0.8～0.9 0.8～0.9 0.8～0.9	Upper Cretaceous (Campanian) of western Montana, USA	Hirsch and Quinn (1990)
Prismatoolithus hukouensis	140	56	0.7～1.0	Upper Cretaceous (Maastrichtian) of Nanxiong Basin, Guangdong, China	Zhao (2000)

2.1　伤齿龙蛋平卧埋在沙土中的受力特征

假设伤齿龙在产卵时是把卵随意平放埋在沙土中,此时蛋的长轴与地面平行。蛋壳沿侧向受到分布压力作用,蛋的钝端和尖端所受的压力可以不考虑,因而不必研究这两个端头的受力特征,只需研究蛋的中段部分在分布压力作用下的抗失稳特征。由固体力学的壳体稳定性研究(Hyman and Healey, 1967)得到用于计算薄壳的失稳临界压力公式为:

$$p_{\phi cr} = (KE/1 - \mu^2)(h/R)^2, \tag{1}$$

式中的 E 为蛋壳材料的弹性模量，h 为壳厚，R 为壳半径，μ 为泊松比。鸟蛋壳材料的 μ 一般为 0.25；如上所述，伤齿龙蛋壳材料和鸟蛋壳的基本相似，故伤齿龙蛋壳材料的泊松比 μ 为 0.25。系数 K 由图 5 查得，图中 b 为蛋的长度。

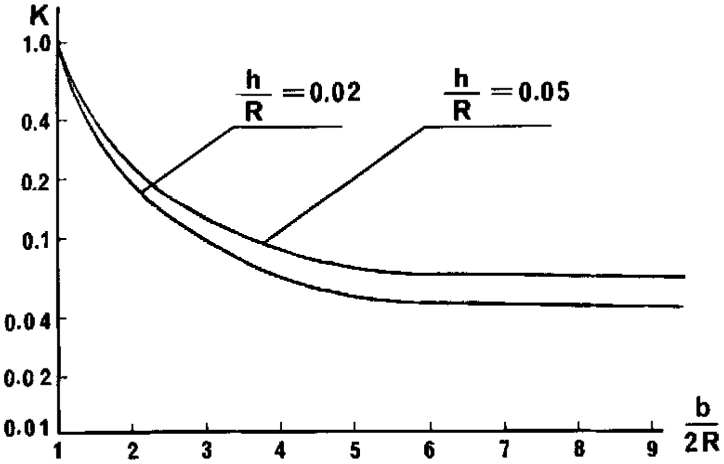

图 5 外压临界载荷系数 K 随形状变化曲线

Fig. 5 Variations in the coefficient K with the b/R

在求得 $p_{\phi cr}$ 后，可根据壳的薄膜理论求得产生凹陷屈曲时壳中的临界应力：

$$\sigma_{\phi cr} = p_{\phi cr}R/h。 \tag{2}$$

有关 6 种伤齿龙蛋的临界外压 $p_{\phi cr}$ 及其临界应力 $\sigma_{\phi cr}$ 等数据计算结果如表 2 所示。

表 2 已知的 6 种伤齿龙蛋的临界外压 $p_{\phi cr}$ 及临界应力 $\sigma_{\phi cr}$ 比较

Table 2 Representive parameters of six types of troodontid eggshells

Name of the eggs	Radius (R) mm	Eggshell thickness (h) mm	h/R	L/2R	K	$p_{\phi cr}$	$\sigma_{\phi cr}$
Prismatoolithus coloradensis	30	0.7	0.023	1.8	0.21	$1.22\times10^{-4}E$	$0.00523E$
Prismatoolithus sp.	24	0.6	0.025	2.4	0.17	$1.13\times10^{-4}E$	$0.00453E$
Prismatoolithus gebiensis	25	0.7	0.028	2.4	0.17	$1.42\times10^{-4}E$	$0.00507E$
Prismatoolithus levis	32.5	0.85	0.026	2.1	0.19	$1.39\times10^{-4}E$	$0.00531E$
Troodon cf. *T. formosus*	33	0.8	0.024	2.3	0.175	$1.10\times10^{-4}E$	$0.00453E$
	30.5	0.8	0.026	1.9	0.20	$1.47\times10^{-4}E$	$0.0056E$
	31	0.8	0.026	1.9	0.20	$1.42\times10^{-4}E$	$0.0055E$
Prismatoolithus hukouensis	28	0.7	0.025	2.5	0.165	$1.10\times10^{-4}E$	$0.0044E$

根据对鸟蛋壳的统计，其失稳屈曲应力 $\sigma_b = 0.025E$（赵资奎、马和中，1997）。从表 2 可以看出，本文研究的 6 种伤齿龙蛋的失稳屈曲应力 $\sigma_{\phi cr}$ 在 $0.0044E$～$0.0056E$ 之间，说明 $\sigma_{\phi cr} < \sigma_b$。很明显，这 6 种伤齿龙蛋壳只要其应力达到 $\sigma_{\phi cr}$ 就会发生破裂。因此，如果把这些伤齿龙蛋平放埋在沙土中就可能在很小载荷下因屈曲而破裂。

2.2　伤齿龙蛋竖立埋在沙土中的受力特征

如果把伤齿龙蛋竖立起来埋在沙土中,此时蛋的长轴垂直于地面,蛋的钝端和尖端这两个端头上分别受到上部和下部传来的分布压力的作用,造成两个端头在外压力下失稳(屈曲);蛋的中段部分也由于要支撑两个端头承受轴向的压力而出现失稳(屈曲)的可能。对于松散的沙土来说,可略去侧向分布压力的影响。研究表明,如果恐龙蛋的长轴垂直于地面,在垂直压力作用下,蛋的中段部分抗失稳压力比两端的小(赵资奎、马和中,1997),容易失稳破裂,因此本文只研究伤齿龙蛋中段部分的抗失稳压力。由公式可得到伤齿龙蛋中段部分能承受的临界总压力:

$$P_{xcr} = 2\pi CEh^2, \tag{3}$$

式中 h 为蛋壳厚度,C 可由以下公式(Weingarten et al., 1965)求得,

$$C = 0.606 - 0.546[1 - \exp(-1/16\sqrt{R/h})], \tag{4}$$

其相应的外力为:

$$p_{xcr} = P_{xcr}/\pi R^2 = 2C(h/R)^2 E, \tag{5}$$

应力为:

$$\sigma_{xcr} = P_{xcr}/2\pi Rh = ChE/R。 \tag{6}$$

根据(3)、(5)及(6)式可以计算出本文研究的 6 种伤齿龙蛋以竖立方式埋在沙土中的临界压力 p_{xcr} 和临界应力 σ_{xcr},计算结果见表 3。

表 3　伤齿龙蛋中部锥体壳轴压 P_{xcr}、p_{xcr} 及 σ_{xcr}

Table 3　Representive parameters of the egg's middle portion of six types of troodontid eggshells

Name of the eggs	C	P_{xcr}	p_{xcr}	σ_{xcr}
Prismatoolithus coloradensis	0.423	$1.30E$	$4.61\times10^{-4}E$	$0.98\times10^{-2}E$
Prismatoolithus sp.	0.428	$0.97E$	$5.35\times10^{-4}E$	$1.07\times10^{-2}E$
Prismatoolithus gebiensis	0.436	$1.34E$	$6.83\times10^{-4}E$	$1.22\times10^{-2}E$
Prismatoolithus levis	0.431	$1.96E$	$5.89\times10^{-4}E$	$1.13\times10^{-2}E$
Troodon cf. *T. formosus*	0.425	$1.71E$	$5.0\times10^{-4}E$	$1.03\times10^{-2}E$
	0.431	$1.73E$	$5.93\times10^{-4}E$	$1.13\times10^{-2}E$
	0.430	$1.73E$	$5.74\times10^{-4}E$	$1.11\times10^{-2}E$
Prismatoolithus hukouensis	0.428	$1.32E$	$5.35\times10^{-4}E$	$1.07\times10^{-2}E$

从表 2 及表 3 列出的 6 种伤齿龙蛋蛋壳的失稳临界压力及应力等数据的比较可以看出,如果把这些蛋平放埋于沙土中,能够承受的分布压力在 $1.10\times10^{-4}E$～$1.47\times10^{-4}E$ 之间;如果把蛋竖立起来埋在沙土中,则可承受的分布压力在 $4.61\times10^{-4}E$～$6.83\times10^{-4}E$ 之间。也就是说,蛋的抗失稳能力比把它们平放埋在沙土中大约高出 4～5 倍。

伤齿龙蛋壳很薄,在 0.6～1.0mm 之间。这种蛋壳的抗失稳能力很差,只有把它们竖立起来埋在沙土中才可能得到最佳的抗压效果,降低它们受压破损的危险程度。因此,为了保证卵在孵化期间能有效地防止蛋壳受压破损,伤齿龙必须从筑巢行为上来改善它们所产的卵的存放状态,以克服蛋壳结构本身的弱点。

伤齿龙属于一种小型、很像鸟类的兽脚类恐龙,于 19 世纪 50 年代首次在北美西部发现。但是,到 20 世纪 80 年代以后,才对它们身体的解剖构造、系统位置和生活习性以及它们的地理分布有了较清楚的了解(Currie, 1987;Lambert, 1993;Xu et al., 2002)。这类恐

龙两腿细长,善于奔跑;有一条挺直的长尾巴,而且在它的身上还可能长有羽毛(徐星,2002)。更有意义的是伤齿龙具有一双略为向前注视猎物的大眼,脑子相对较大,说明伤齿龙智商较高。因此,有理由认为,伤齿龙产卵时,把一个个蛋竖立起来埋在沙土中是非常必要的和可能的。这种筑巢产卵的行为可以保证胚胎在正常情况下能够顺利发育。

3 伤齿龙蛋窝的大小

根据Horner和Gorman(1988)的报告,北美蒙大拿地区西部发现的伤齿龙蛋(当时以为

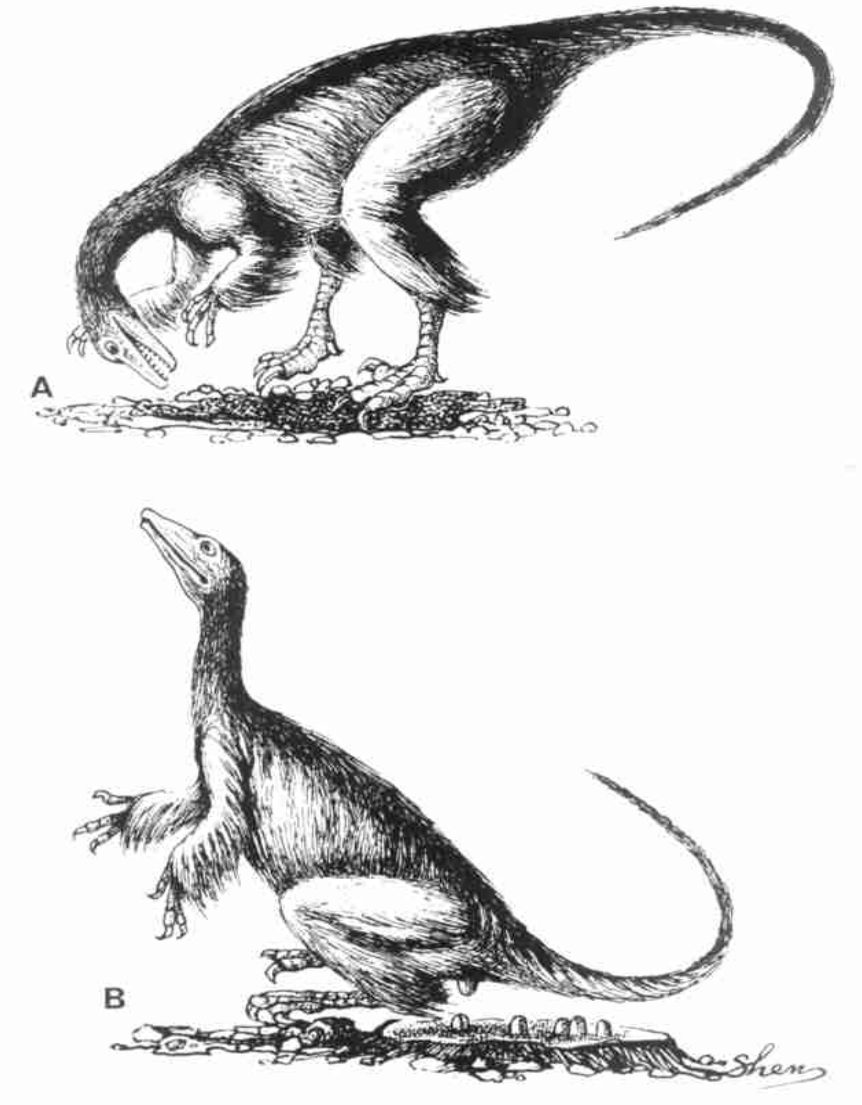

图6 中国白垩纪伤齿龙筑巢产卵行为复原

Fig. 6 Nesting behavior of the Chinese Cretaceous troodontid

A. 松土构筑巢穴 building nest;B. 产卵 the squatting female laying her eggs

是属于棱齿龙的)主要集中分布在两个各宽约70m的地方。每个蛋窝直径1m左右,蛋窝之间的距离为2～3m。通常每个蛋窝含有12到19枚蛋不等,最大的蛋窝含有24枚蛋,也就是说,一条伤齿龙一次产卵可多达24枚左右。所有的蛋都是直立或斜插在泥质灰岩中,说明当时生活在这一地区的伤齿龙是以干涸了的沼泽或湖底作为产卵的地点。它们可能利用每年某个干燥时期,在那些地势较高的湖底或沼泽地露出水面后便成群来到那里,不需要构筑土堆或洞穴就能把产出的卵直立或稍微倾斜地插入含有腐植质的湿润泥土中。

根据上述对伤齿龙蛋壳的力学性质分析,显而易见,伤齿龙选择这种环境作为产卵地点,可以不必构筑特别的巢穴就能直接把卵竖立在比较湿润的泥土中。但它们要把产出的卵直立或稍微倾斜地插入泥土中,就必须使其身躯保持半直立状态,靠输卵管向下蠕动的力量把卵压入泥土中。

这里要特别指出的是,Hirsch 和 Quinn (1990) 在研究这些蛋壳结构时,注意到蛋壳外表面上具有平行、纵向的细纹(Hirsch and Quinn, 1990, 图3E-F),并将它作为这类蛋壳的特征。根据蛋壳在输卵管中形成的机理,对此很难做出合理的解释。但是从上述伤齿龙的产卵行为来看,可以认为,在这些蛋壳外表面上具有的纵向细纹可能不是蛋壳本身固有的特征,而是当这些卵被压入土中时与其周围泥土磨擦而成的机械擦痕。因此不能把它当作分类标志。

中国发现的伤齿龙蛋窝比北美西部的要小得多,每窝只有6～7枚蛋。这些蛋保存在砖红色粉砂岩中(赵资奎、李荣,1993;王德有、周世全,1995;Zhao,2000),表明以这些蛋化石为代表的伤齿龙是以河湖岸边作为产卵的地点。这就可以看出,中国和北美西部白垩纪伤齿龙产卵地点的地质环境和生殖方式是非常不同的。由于中国白垩纪伤齿龙是选择河湖岸边沙土地作为产卵的地点,它们要在这种环境下产卵,并把卵竖立起来埋在沙土中,就必须构筑巢穴(图6)。首先,伤齿龙要用爪松土。就是说,要先用爪松土构筑巢穴,然后蹲坐下来使其身躯成直立或半直立姿势。这样,依靠输卵管向下蠕动的力量把一个个蛋直立地插入松软的沙土中。

如果一条伤齿龙一次可产卵24枚左右,那么,中国白垩纪的伤齿龙不可能像北美西部的伤齿龙那样可把所有的卵产在一窝中。如上所述,生活在北美的伤齿龙是把卵产在刚露出水面的湖底或沼泽地的湿润泥土里,靠输卵管向下蠕动的力量能较容易地把它们深深插入泥土中。然而生活在中国的白垩纪伤齿龙是选择河湖岸边的沙土地作为产卵地点,在这样的环境下筑巢产卵,很难靠输卵管向下蠕动的力量把一个个蛋竖立起来深深地插入沙土里。为了防备产出的卵倾倒下来,它可能把一次要产的卵分成若干窝。也就是说,中国白垩纪的伤齿龙在产6～8枚卵后,就用爪耙周围的沙土,把这些卵埋起来,然后再筑另一巢穴产卵。

致谢　承蒙徐星博士提供伤齿龙复原图,王德有先生提供河南西峡盆地伤齿龙蛋化石照片,沈文龙先生绘制插图,特此致谢。

THE NESTING BEHAVIOR OF TROODONTID DINOSAURS

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Key words troodontid egg , critical pressure ,critical stress ,instability ,breaking strength ,nesting behavior

Summary

The troodontid eggs have been preserved standing up on the nest ,pointed ends downwards , so that they looked as if they had been stuck in the ground when they were laid (see Fig. 5 of Horner , 1984 ; Fig. 3d of Hirsch and Quinn ,1990 ; Plate I of Zhao and Li ,1993 ; Fig. 1 of Zhao ,2000) . Why did the troodontids put their eggs vertically into the earth at nesting ? Does the nesting behavior have any paleobiological significance ?

The troodontid eggs were initially described as prismatoolithid eggshells by Hirsch and Quinn (1990) from Western Montana ,USA and formally named by Zhao and Li (1993) . These eggs were initially assigned to hypsilophodontid *Orodromeus makelai* ,based on embryonic remains within eggs from Western Montana (Horner and Weshampel ,1988) . However ,it has been announced (Horner and Weshampel ,1996) that the initial identification of these embryos was erroneous. They were re-identified as the small theropod *Troodon* cf. *T. formosus* ,rather than *Orodromeus makelai*.

Based on the fossil record so far available ,the prismatoolithid eggshells are also known from Canada , China , France and Mongolia. Although the eggs from these sites contain no embryonic remains ,the similarity of their eggshell structure and the pattern of the egg arrangement in the nest suggest that the same type of troodontids or closely related species had laid these eggs.

The primary functions of the eggshell are to protect the embryo and to mediate the interaction between the developing embryo and the outside environment. It must be strong enough to withstand the external pressure during its incubation , yet fragile enough to crack easily when the young hatches. Therefore ,it is clear that the mechanical properties of the eggshell have a great influence upon hatchability. When the dinosaur eggs were laid and buried in the earth for incubation ,they were subjected to external pressure. Once the pressure comes to the critical value p_{cr} , the eggshell will subside and then break. It has been demonstrated that the p_{cr} is mainly determined by the geometry of the eggshell (long axis ,radius ,thickness) ,the nature of the eggshell material (elastic modulus ,Poisson 's ratio) and the direction of the external forces acting on it.

According to the theory of thin shell ,the critical pressure p_{cr} and critical stress σ_{cr} of troodontid eggshell can be obtained when the egg is buried oriented horizontally or vertically in the earth (Tables 2 and 3) .

The troodontid eggshell is very thin. Its ability to resist buckling (or instability) is very poor , and the eggs can merely bear pressure $p_{\phi cr} = 1.10 \times 10^{-4} E \sim 1.47 \times 10^{-4} E$ (Table 2) if they are horizontally buried in the earth. However ,when the eggs are put standing up vertically in the earth , the external pressure p_{xcr} they are subjected to can be $4.61 \times 10^{-4} E \sim 6.83 \times 10^{-4} E$ (Table 3) . That is to say ,the eggshell ability to resist buckling will be four to five times as compared with that of the egg oriented horizontally. It is reasonable ,therefore ,that the troodontid dinosaurs had to arrange their eggs vertically or somewhat obliquely in the earth at nesting , in order to prevent the eggshell from being crushed by the external pressure during the incubation.

Troodontid dinosaurs are a group of small ,bipedal ,bird-like theropod with keen eyesight and a relatively large brain ,indicating a high level of intelligence. Besides ,they probably had feathers on its

body(Xu ,2002) . It is necessary and achievable that these animals place their eggs standing up vertically in the earth when they are laid.

The eggs from the western Montana have been preserved standing up ,vertically or obliquely in mudstone ,suggesting that troodontid dinosaurs could take dried lake bed as their nesting site (Horner and Gorman 1988) . When the lake was high (and these kinds of lakes tended to dry up each year) they would have come and laid their eggs. It seems that they did not make nests ,that is to say ,they did not build special place to lay their eggs. It is quite obvious that in such geological environment the troodontids are able to put their eggs vertically into the muddy soil and need not construct a special place for them. However ,they had to lay their eggs from squatting position ,and by the peristalsis of the oviduct the eggs were forced into the muddy soil.

It is worth mentioning the fact concerning the fine parallel striations on the outer surface of the eggshell belonging to *Troodon* cf. *T. formosus* (see Fig. 3E-F of Hirsch and Quinn ,1990) . Judging from this , I would rather think that the above-mentioned longitudinally oriented striations on the eggshell surface that were described as a taxonomic character (Hirsch and Quinn ,1990) could not be the natural sculpturing ,but should be produced by rubbing when the egg was forced into the sediment. Thus ,it cannot be used as a taxonomic indicator of the troodontid eggshells.

The troodontid eggs , *Prismatoolithus* ,found in China have been preserved in siltstones ,indicating that the troodontids represented by these eggs chose lakeside or riverine sands as their nesting sites. Each clutch contains 6～7 eggs. It will not be surprising to infer ,however ,that under this environmental conditions the troodontids must first loosen the sediments to make the special place and then squat down to lay their eggs (Fig. 6) . After laying 6～8 eggs ,she might easily manipulate one or two slippery eggs ,and then cover them with sands.

As has been shown above ,each of troodontid nests found in China contains only 6～7 eggs. However , Horner (1984) reported finding clutches of up to 24 eggs per nest in Montana ,indicating that a single female troodon was able to produce eggs as many as 24 or more at one laying. The Chinese troodontids preferred to lay their eggs in the lakeside or riverine sands. Under the circumstances the troodontids could hardly construct a special nest more than one meter in diameter for laying and putting them vertically into the sands. It was likely that the female produced a total of perhaps 24 eggs but she separated them in several clutches.

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