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贵州寒武纪始海百合类萼部形态定量评价及其意义*

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提要　始海百合类是贵州寒武纪杷榔动物群和凯里生物群代表性化石类群。产出杷榔动物群和凯里生物群的杷榔组和凯里组主要由灰绿色、灰色的泥、页岩组成,始海百合类化石保存在 2 个组中上部的泥、页岩中,化石保存好,丰度高,是陆棚斜坡较深水环境生态类群的典型代表。本文基于来自杷榔组的 36 块 *Guizhoueocrinus yui*,29 块 *Protogloboeocrinus yini* 标本,和凯里组的 20 块 *Sinoeocrinus lui*,20 块 *Globoeocrinus globulus* 标本,采用几何形态测量方法和传统形态测量方法,对每块标本萼部选定了 4 个界标点(landmark),进行数理统计和几何形态的定量分析。发现寒武纪始海百合类的萼部尺寸上差异较小,在形态上,杷榔组的 *Protogloboeocrinus yini* 和 *Guizhoueocrinus yui* 萼形相似,均偏细长形,而凯里组的 *Sinoeocrinus lui* 和 *Globoeocrinus globulus* 萼形差异较大,口部区域宽度均出现增大,萼茎连接处宽度则出现变大和变小两种趋势。结果说明:同一生态环境下寒武纪早期的 *Guizhoueocrinus yui*,和中期的 *Sinoeocrinus lui* 的萼在演化上具连续性,细长的萼与长茎能够让始海百合个体更有效捕食上部水域的食物,而寒武纪早期的 *Protogloboeocrinus yini* 和中期的 *Globoeocrinus globulus* 的萼在形态上具有演化上的连续性。球状的萼配合粗短的茎,可以增强始海百合个体的稳定性,以适应更强的水动力环境,表明出现了生态位的扩张。

关键词　始海百合类　几何形态测量　杷榔组　凯里组　寒武纪　贵州

1　前　言

始海百合的身体结构可分为腕枝、萼、茎、吸盘 4 部分(赵元龙等,1994;毛永琴等,2007;闫旭等,2010;Durham,1978;Zhao *et al.*,2007,2008),亦有研究者将茎与吸盘统称为固着器(holdfast 或 stalk)(Sprinkle,1973;Parsley and Prokop,2004)。萼是始海百合最重要的器官,萼的内部含有司营养、呼吸、消化等作用的内脏与水管系统,还是支持个体在水中浮动的重要器官,故萼的形态研究对弄清始海百合个体发育与环境的协同演化具有重要意义(Sprinkle,1973)。始海百合类最早在 1921 年被 Jaekel(1921)设立为单独的类群,置于海百合纲下的海蕾亚纲。中国南方的贵州寒武纪杷榔动物群和凯里生物群是陆棚深水环境发现的重要的布尔吉斯页岩型生物群,2 个生物群的类群组成多样、均以始海百合类为特征类群,为杷榔动物群和凯里生物群代表性的化石类群,保存好,丰度高,是陆棚斜坡较深水环境生态类群的典型代表(赵元龙等,1999;Peng *et al.*,2005;Feng *et al.*,2006)。而同在中国南方浅水台地区的云南澄江生物群、关山生物群的始海百合化石类群少,保存差,丰度低(黄迪颖,2012;Hu *et al.*,2007)。这可能是由于始海百合类喜宁静深水环境的生态特征导致(Parsley and Prokop,2004)。杷榔组和凯里组都形成于贵州寒武纪的陆棚斜坡带(周志毅等,1979;尹恭正,1987;Peng and Babcock,2001)。前者时代为寒武纪第 4 期(彭善池,2005),后者的时代为寒武纪第 5 期(Zhao *et al.*,2005)。

杷榔组确认有始海百合类 2 属 2 种 *Guizhoueocrinus yui* Zhao,Parsely and Peng,2007,*Protogloboeocrinus yini* Zhao,Peng and Wu,2015(赵元龙等,2015;Zhao *et al.*,2007;插图 1A,1B)。

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凯里组也确认有 2 属 2 种 *Sinoeocrinus lui* Zhao, Huang and Gong, 1994, *Globoeocrinus globulus* Zhao, Parsely and Peng, 2008(赵元龙等, 1994; Zhao *et al*., 2008; 插图 1C, 1D)。前人研究认为, 杷榔组的 *G. yui*, *P. yini* 和凯里组 *Gl. globulus*, *S. lui* 在形态和时代上有较明显演化关系(赵元龙等, 2015; Zhao *et al*., 2007; Parsley, 2012)。杷榔组的 *G. yui* 和凯里组的 *S. lui* 萼较相似, 均为细长的锥形到长椭圆形(赵元龙等, 1994; Zhao *et al*., 2007; Parsley, 2009); 而杷榔组的 *P. yini* 则被认为是凯里组 *Gl. globulus* 的原始属种, 均有椭球形或近于球形的萼(赵元龙等, 2015)。

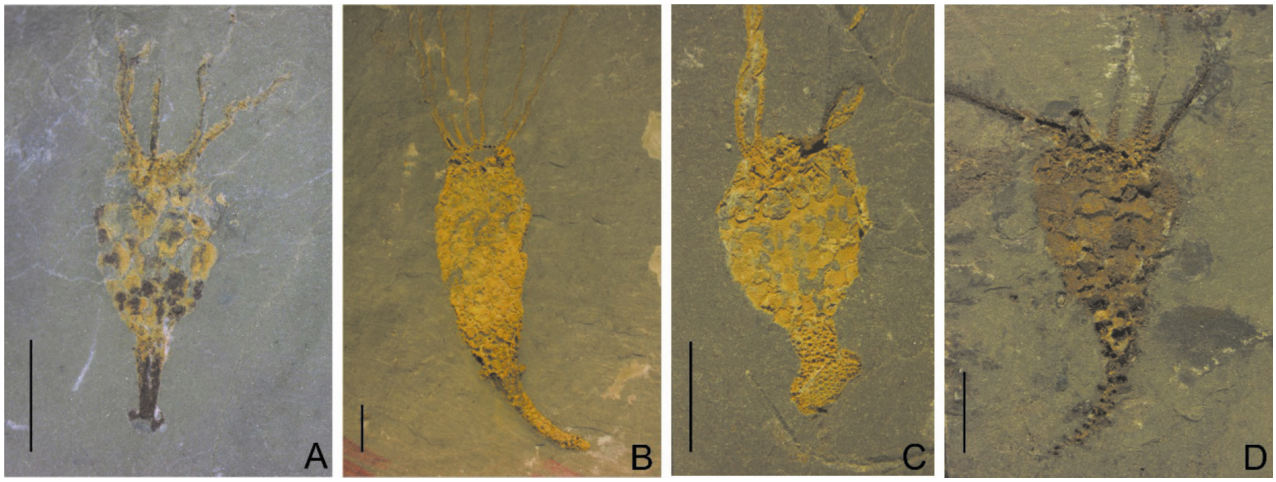

插图 1 贵州寒武纪杷榔组和凯里组的始海百合类化石

Eocrinoid fossils from the Cambrian Balang and Kaili formations of Guizhou

A. *Protogloboeocrinus yini* Zhao, Peng and Wu, 2015, 标本号: GY-266-4; B. *Guizhoueocrinus yui* Zhao, Parsely and Peng, 2007, 标本号: KP-3-101; C. *Globoeocrinus globulus* Zhao, Parsely and Peng., 2008, 标本号: GBG-599; D. *Sinoeocrinus lui* Zhao, Huang and Gong, 1994, 标本号: GM-16-140。A 和 B 产自杷榔组; C 和 D 产自凯里组。图上所有比例尺线条等于 5 mm。

A. *Protogloboeocrinus yini* Zhao, Peng and Wu, 2015, Specimen No.: GY-266-4; B. *Guizhoueocrinus yui* Zhao, Parsely and Peng, 2007, Specimen No.: KP-3-101; C. *Globoeocrinus globulus* Zhao, Parsely and Peng, 2008, Specimen No.: GBG-599; D. *Sinoeocrinus lui* Zhao, Huang and Gong, 1994, Specimen No.: GM-16-140. A-B. Yielding in the Balang Formation; C-D. Yielding in the Kaili Formation. All scales bars on pictures equal 5 mm

本次研究选取上述 4 个种, 总计 105 块保存完整的化石标本。采用传统形态测量(traditional morphometrics)与几何形态测量(geometric morphometrics)的方法进行统计分析, 用以确认 4 个种萼的形态变化、分类学意义及萼在演化上趋异与生态位扩张的相关性。

2 材料与方法

2.1 材料

材料源自团队长期野外工作采集的标本: *P. yini* 29 块, *G. yui* 36 块, *S. lui* 和 *Gl. globulus* 各 20 块, 分别选自 Parsley 和 Zhao(2006)和 Zhao 等(2008)发表的文章中所用的标本。

被选用的标本要求茎和萼间结构完整, 基本忽略埋藏偏差对萼部形态变异产生的影响。所有化石标本保存在贵州大学贵州省古生物研究中心。

2.2 数据采集

使用超景深三维显微系统 VHX-100K 拍摄化石标本数码照片, 并在 CorelDRAW2017 中对所有化石照片统一比例尺, 将其导入 tps-DIGl. 40 (Rohlf, 2004a, 2004b)中并按逆时针顺序在萼的口部区域和底部共设定了 4 个界标点(landmark)(插图 2, 附录 Ⅰ)。同时也采用传统形态测量(traditional morphometrics)手段来展示萼的形状变化规律, 而 3 个传统测量度分别为萼高(Thecal height, TH), 萼宽(Thecal width, TW)与茎高(Stem height, SH)(附录 Ⅱ)。以上数据在 Digimizer 软件中测量化石标本的数码照片获得。

2.3 方法

几何形态测量方法: 几何形态测量是一种基于笛卡尔坐标的统计学分析方法, 通过在化石上设立界标点、半界标点, 更全面地从化石上提取形态信息来进行相关分析(Rohlf and Marcus, 1993; Rich-

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tsmeier *et al.*, 2002; Adams *et al.*, 2004; Mitteroecker and Gunz, 2009; Zelditch *et al.*, 2012)。Bookstein(1991)提出，界标点共分为 3 类，一型标点(Type Ⅰ landmark)是指不同组织间的交点，能被精确定位，可能具有生物学上"同源"的意义；二型标点(Type Ⅱ landmark)是指结构中的凹陷或突起点，可以用来推论功能及作用；三型标点(Type Ⅲ landmark)是指结构的极点，可靠程度较低(Bookstein，1990)。这里通过使用 Tps-Dig v2. 16 软件在萼部按顺时针方向设立 4 个界标点(插图 2A)，以便描述某种特定的萼部形态。

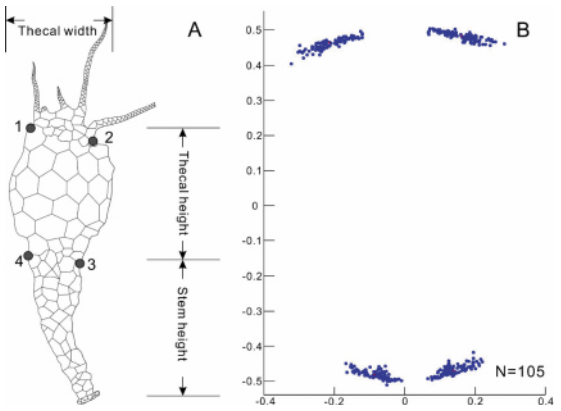

插图 2　始海百合类素描图及叠印图

Sketch plot and superimposition plot of eocrinoids

A. 单一始海百合类个体体构素描图及所选萼部界标点位置示意图，B. 105 块始海百合标本萼部界标点的普氏叠印图。

A. Reconstruction of an eocrinoid individual, showing the locations of landmarks on theca, B. superimposition plot of 4 landmarks on theca from 105 eocrinoid specimens.

据化石标本采集到的原始形态坐标数据首先被导入 PAST3 软件(Hammer *et al.*, 2001)，生成方差-协方差矩阵(Bookstein, 1991)。为了统一每个化石标本的位置、大小与方向，我们在 PAST3 里对每个样本的形态坐标进行普氏转换，所有的笛卡尔形态坐标按照普鲁克迭加(Procrustes superimposition)被转换成为普氏形态坐标(Goodall, 1991; Hammer and Harper, 2006)。

主成分分析(PCA)方法的基本原理是通过坐标的回归变换，将原有(多个)变量的绝大部分变化(即方差或协方差)集中用少数变量表达出来，以便更直观、单一地表现研究样本之间的关系(Macleod, 1999)。典型变量分析(CVA)是多变量分析中进行判别分析的一个重要方法，可以用于多组数据之间的判别。CVA 所作的坐标转换，在于"拉近"样本组的组内差异，"突出"组间差异(Campbell and Atchley, 1981; Macleod, 2007)，即将各组样本之间的差别用最显著的方式展示出来以供判别。

为了能够观察 4 个种萼部形态间的关系，我们在 PAST3 软件里对普氏坐标矩阵采用多元变量统计分析。首先运用主成分分析来比较 4 个种的种间差异，在主成分分析的基础上，为了更好地观察到组间差异，采用典型变量分析(CVA, Campbell and Atchley, 1981; Macleod, 1999)和多元方差检验(MANOVA)，用以判断萼部形态的差异以及是否具有显著性(Webster and Sheets, 2010)。

薄板样条(Bookstein, 1989, 1991)是一种产生光滑样条的数学模型，用来描述样本从参考形(the reference form)到目标形(the target form)的形态变化。通常用于描述两个形状之间的差异性，原理是寻找一个通过所有形态控制点且形变后弯曲度最小的光滑曲面，这个光滑曲面可以通过最小能量函数获得(Bookstein, 1989)。这里在 PAST3 软件里创建了薄板样条模型(TPS, Bookstein, 1989, 1991, 1996)，对普氏形态坐标矩阵进行薄板样条分析，绘出 4 个种萼部平均形态的网格变形图，可直观地对杷榔组的 2 个种间和凯里组的 2 个种间的平均形态上的差异进行比较。

传统形态测量方法：包括对一系列形态学测量度数据进行统计分析(Blackith and Reyment, 1971; Marcus, 1990)。通常使用的是线性距离、比值、角度等。通过多组传统测量度数据的统计分析，可以找出不同形态特征的变化规律，并与几何形态测量的结果相互印证。这里测量了每个个体的萼高、萼宽、茎高的数据，用以阐释杷榔组的 2 个种及凯里组的 2 个种的个体发育情况和萼部形态的演化趋势(插图 3)。

3　萼部形态特征

3.1　传统形态度量

为了避免个体发育过程中萼部形态变化对我们判断种间的萼部形态变化产生干扰，我们先对每个种在个体发育过程中的萼部形态变化进行双变量统计分析。

基于杷榔组 *P. yini* 29 块标本和 *G. yui* 36 块标本，以及凯里组 *Gl. globulus* 20 块标本和 *S. lui* 20 块标本(这些标本包括幼年和成年个体)，我们绘制了萼高与萼宽的散点图并对数据进行回归分析，发现这 4 个种的萼高与宽均呈正相关，随着萼高的

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增长，萼宽相应地按一定比例增长，相关系数较高（$R_1=0.88503$，$R_2=0.95266$，$R_3=0.95344$，$R_4=0.92483$）（见插图 3，表Ⅰ）。4 个种萼的宽与高的比值近似恒定，确认同一个种在个体发育过程中萼部的形态未发生大的变化。

3.2 几何形态度量

质心距（Centroid size）：质心距是几何形态度量中最常用的尺寸测度，计算方法是每个界标点到质心距离平方和的平方根。由于它不会引入尺寸大小和形态之间的相关性，通过计算萼部质心距的变化，我们可以对单一种的萼部形态的大小进行探讨（Mitteroecker and Gunz，2009）。

Globoeocrinus globulus，*S. lui*，*P. yini* 和 *G. yui*，4 个种萼部质心距的分布情况见插图 4。杷榔组 *P. yini* 和 *G. yui* 的萼部质心距大小集中于 0—6 000 mm，而凯里组 *Gl. Globulus* 和 *S. lui* 的质心距的变化范围在 0—9 000 mm，出现了微弱的扩大，但均值与中位数均较为相近。表明在个体发育过程中，时代晚的 *Gl. globulus*，*S. lui* 的萼大小和时代早的 *P. yini* 与 *G. yui* 的萼大小大致相同，体现了始海百合类萼在演化过程中的演化趋势。

主成分分析（PCA） 为了直观表现化石样本形状之间的关系，我们对基于普氏形态坐标的方差-协方差矩阵进行主成分分析。主成分分析可展示出杷榔组 *P. yini*，*G. yui*，和凯里组 *Gl. globulus*，*S. lui*

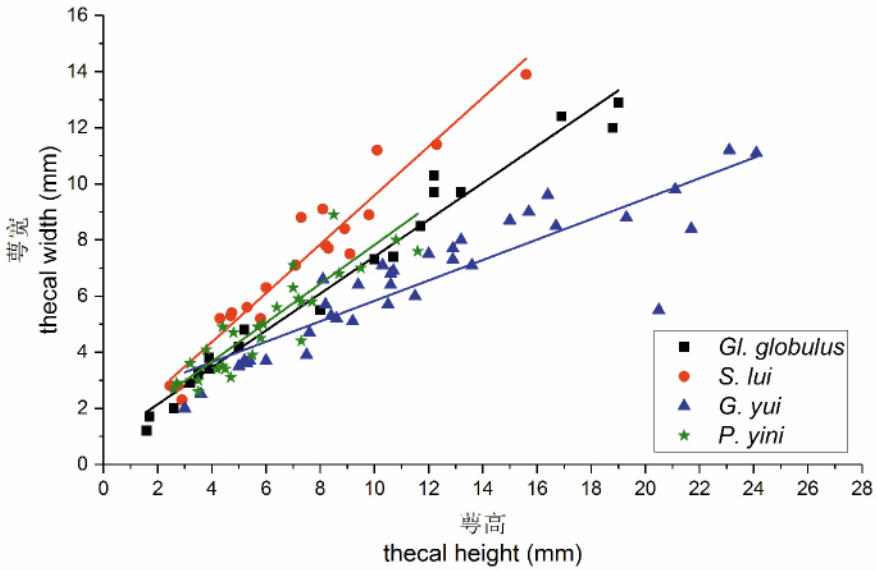

插图 3 杷榔组 *Protogloboeocrinus yini*，*Guizhoueocrinus yui* 与凯里组 *Globoeocrinus globulus*，*Sinoeocrinus lui* 的萼高-萼宽散点图及 OLS 模型线性回归

Scatter plot and OLS model liner regression between TH-TW of *Protogloboeocrinus yini*, *Guizhoueocrinus yui* from the Balang Formation and *Globoeocrinus globulus*, *Sinoeocrinus lui* from the Kaili Formation

表Ⅰ 杷榔组的 *Protogloboeocrinus yini*，*Guizhoueocrinus yui* 与凯里组 *Globoeocrinus globulus*，*Sinoeocrinus lui* 的萼高-萼宽 OLS 线性回归参数（问号后数值为标准误差）

OLS Linear regression function of TH-TW of *Protogloboeocrinus yini*, *Guizhoueocrinus yui*, *Globoeocrinus globulus* and *Sinoeocrinus lui* and their regression parameters (values behind the question mark are standard errors)

Equation	$y=a+b*x$			
Plot	*Gl. globulus*	*S. lui*	*G. yui*	*P. yini*
Intercept	0.8246 ? 0.24244	0.87164 ? 0.43325	2.18793 ? 0.41509	0.89187 ? 0.45763
Slope	0.65772 ? 0.02414	0.87137 ? 0.05496	0.364 ? 0.03189	0.6929 ? 0.07014
Residual Sum of Squares	3.26398	11.39869	39.085	20.96379
Pearson's r	0.98809	0.96602	0.89051	0.88503
R-2	0.97632	0.93319	0.79301	0.78329
Adj. R-Square	0.975	0.92948	0.78692	0.77526

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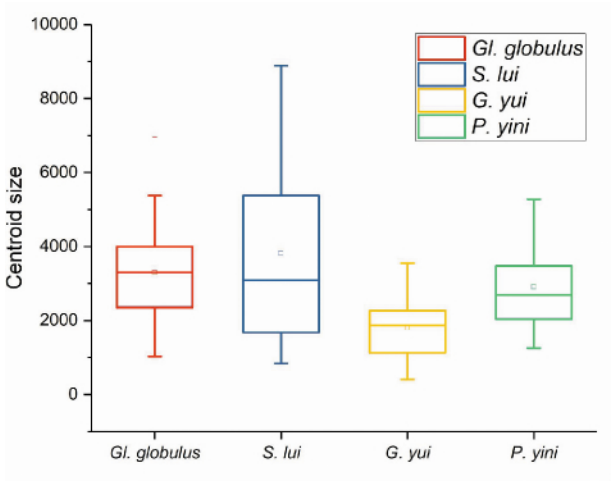

插图 4　贵州寒武纪始海百合类 4 个种萼部质心距分布图

Plots of the individuals examined data of centroid size of theca from 4 Cambrian eocrinid species in Guizhou

4 个种萼部形态上的种间差异(插图 5)。插图 5 展示了沿 3 条主成分轴观察到的萼部形态的变化状况。前三个主成分占比总和为 98.904%,能够较为完整地展示出原始矩阵中的数据信息。其中,PC1 占比 82.648%,PC2 占比 15.113%,PC3 占比 1.143%。

PCA 展示了来自杷榔组与凯里组的始海百合类 4 个种萼部形态的属种间有差异。图中 3 个种的重叠区域过多,难以找出 3 个种之间存在的差异。可以看出 *Gl. globulus*,*P. yini*,*G. yui* 在萼部形态上较为相近,其中 *Gl. globulus* 和 *P. yini* 距离更近,而 *S. lui* 与其他 3 个种存在明显差异。为了能够更好地找出始海百合萼部形态的种间关系,我们对普氏形态坐标矩阵继续采用典型变量分析(CVA),见插图 6。

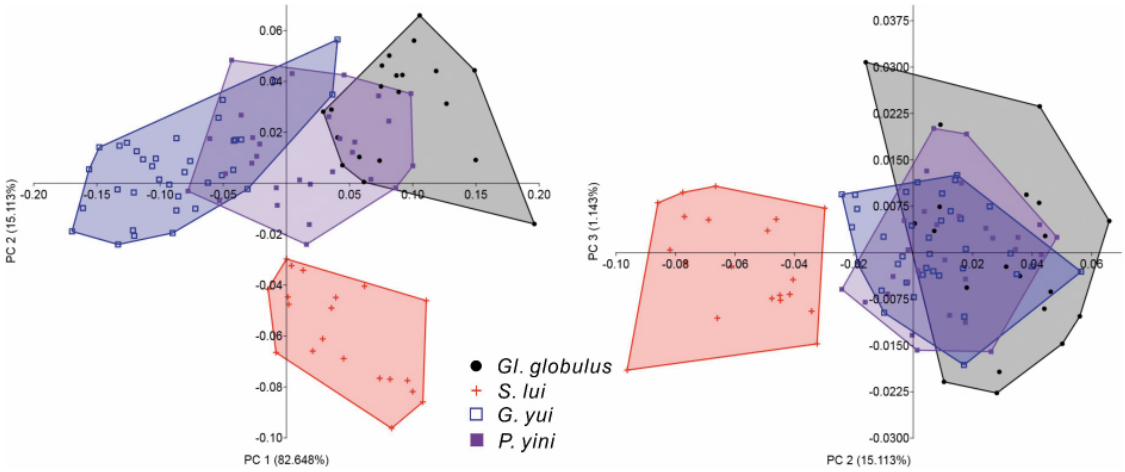

插图 5　贵州寒武纪始海百合类 4 个种萼的主成分分析图(PCA)及各主成分形态变形网格

Principal component analysis(PCA) and deformation grids in each PCs of theca from 4 Cambrian eocrinoid species in Guizhou

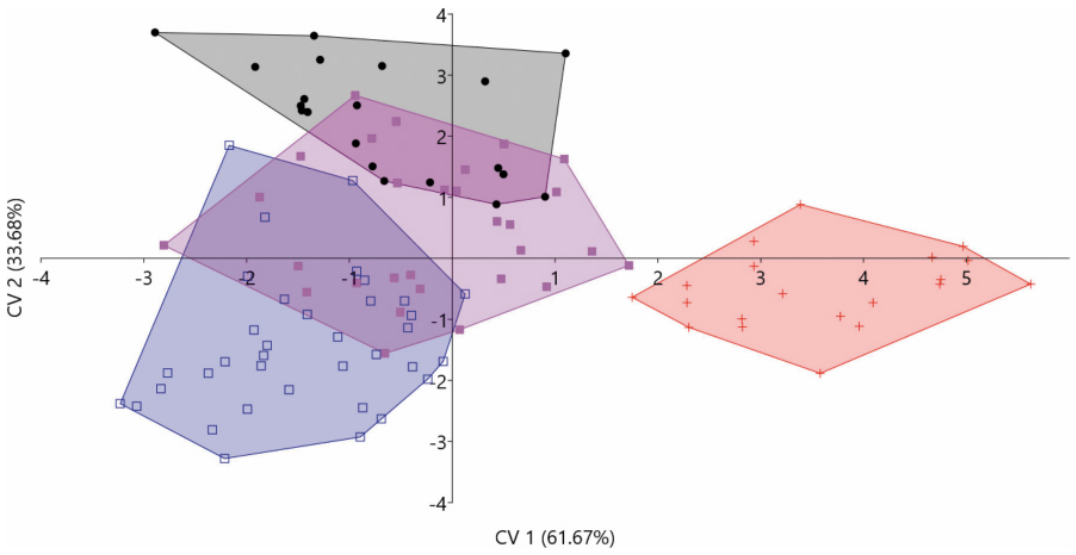

插图 6　贵州寒武纪始海百合类 4 个种萼部典型变量分析图(CVA)

Canonical variate analysis(CVA) of theca from 4 Cambrian eocrinoid species in Guizhou

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典型变量分析是多变量分析中进行判别的方法，可以拉近组内差异而放大组间差异（Cambell and Atchley，1981；Macleod，2007），为验证 CVA 结果是否具有显著性，我们在 CVA 的结果上进行多元方差分析（MANOVA）。CVA 和 MANOVA 提供了 2 个能够显著区分的典型变量（Wilk's lambda：0.05911，df1：24；df2：273.3；F：18.8；P-value：9.887E-45；Pillai trace：1.649；df1：24；df2：288；F：14.65；P-value：3.983E-37）。

CVA 图展示了贵州寒武纪始海百合类 4 个种萼部形态的种间分异。从图中可知，*Sinoeocrinus lui* 与其他 3 个种有最明显的差异。杷榔组的 *G. yui* 与 *P. yini* 2 个种萼形差异相对较小，而凯里组的 *S. lui* 有着较为细长的萼部，*Gl. globulus* 的萼部形态趋向于球形；相较杷榔组的 2 个种，凯里组的 2 个种的萼部形态出现了较大的趋异现象。Hotelling's p 值（即未对多次检验进行修正），Bonferroni 修正 p 值（即 p 值乘以成对比较的数目）见表Ⅱ。

表Ⅱ 贵州寒武纪始海百合 4 个种萼形间每 2 组数据的比较（Hotelling p 值，Bonferroni 修正）

Pairwise comparison of 4 Cambrian eocrinoid species (Hotelling p-values, Bonferroni corrected)

	Globoeocrinus globulus	*Sinoeocrinus lui*	*Guizhoueocrinus yui*	*Protogloboeocrinus yini*
Globoeocrinus globulus	0	2.5593E-11	1.6627E-12	5.1159E-05
Sinoeocrinus lui	2.5593E-11	0	4.2247E-17	2.2389E-11
Guizhoueocrinus yui	1.6627E-12	4.2247E-17	0	2.0195E-08
Protogloboeocrinus yini	5.1159E-05	2.2389E-11	2.0195E-08	0

薄板样条分析（Thin-plate splines） 为了直观地体现 *G. yui*，*S. lui*，*Gl. globulus*，*P. yini* 4 个种间形态的差异，在普氏形态坐标矩阵中，采用薄板样条变形来比较 4 个种萼部的平均形态，见插图 7。

Globoeocrinus globulus 与 *S. lui* 在萼部平均形态的对比图显示凯里组的始海百合在萼部形态上存在明显的差异。根据图中刻度数值可以判断界标点的相对位置变化（大于 1 代表扩张，小于 1 代表收缩），直线指示平均形态的变化方向，颜色展示了变形网格扩张/收缩的程度。*S. lui* 较 *Gl. globulus* 而言，有着细长的萼部形态，而萼茎连接处的区域更狭窄。同样，杷榔组的 *P. yini* 与 *G. yui*，在萼部形态上差异也比较明显：*G. yui* 在口部区域和萼茎连接处比 *P. yini* 的更狭窄。通过进一步比较 *P. yini* 与 *Gl. globulus* 和 *G. yui* 与 *S. lui*，前者种间差异较小，*Gl. globulus* 的口部区域和萼茎连接处比 *P. yini* 略有扩大，而 *S. lui* 与 *G. yui* 相比，有着相对更宽阔的口部区域。

4 讨 论

始海百合动物的生活方式决定了萼与茎间有着密切的关系，基于 *Gl. globulus*，*S. lui*，*P. yini*，*G. yui* 4 个种，做出萼高-茎高散点图（插图 8）。我们可以看出，除 *Gl. globulus* 外，其余 3 个种的萼高、茎高比值较为接近，从 4 个种茎高的线形图，可发现 *Gl. globulus* 和 *P. yini* 有着较短的茎，更加适应固着在硬底上生活，硬底多是生物的遗体（如：三叶虫碎片、腕足类等）（闫旭等，2010），而 *S. lui* 和 *G. yui* 茎明显较长，更适应锚固在软的砂泥质海底，指示 *S. lui* 和 *G. yui* 之间，*Gl. globulus* 和 *P. yini* 之间在生活方式上分别存在着演化上的相关性。

杷榔组的 *G. yui* 与 *P. yini* 在萼部形态上差异不大，均偏向细长的椭球形，而凯里组的 *S. lui* 与 *Gl. globulus*，萼部形态出现了明显的分异，其中 *S. lui* 与其它 3 个种都有着较大的形态差异：*S. lui* 有类似于 *G. yui* 较为细长的萼，随着个体的增长，萼部形态变化较小，萼高与萼宽之间的比值仅出现了微小的降低，普遍具有较长的茎，萼高与茎高之间的比值也较为恒定；*Gl. globulus* 则有更明显的球状萼部，茎大幅度缩短，而在口部区域 *S. lui* 和 *Gl. globulus* 均出现了明显的扩大。这种萼部形态的趋异现象可能与生存环境的变化相关：功能形态学方面，宽阔的口部区域、细长的萼与茎可扩大生物体的有效捕食面积，更适合于悬浮捕食的生活方式；相应的，球状的萼部配合粗短的茎可以提高始海百合个体的稳定性，使其能够更为稳固地锚固在海洋基底或者动物的碎片上，从而适应更强的水动力环境。

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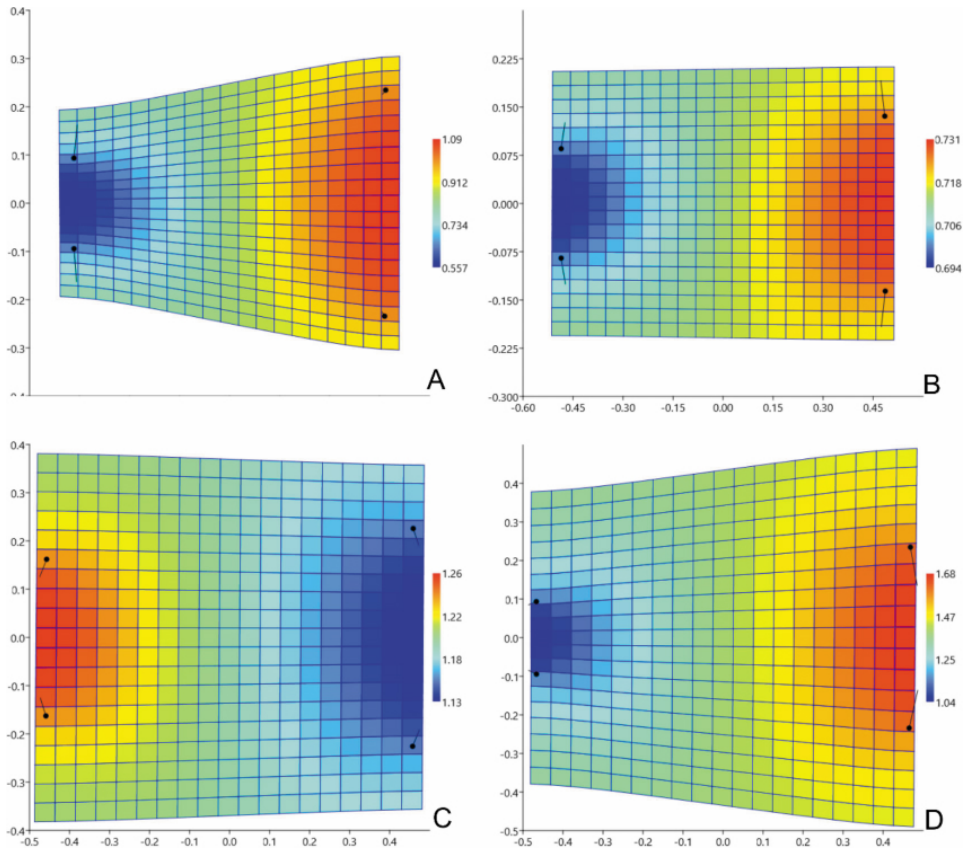

插图 7　贵州寒武纪始海百合类 4 个种的萼部平均形态的薄板样条变形特征

Thin-plate spline deformation of the mean shape of thecae from 4 Cambrian eocrinoid species in Guizhou

A. **从** *Globoeocrinus globulus* **到** *Sinoeocrinus lui* **萼部平均形态的薄板样条变形**;B. **从** *Protogloboeocrinus yini* **到** *Guizhoueocrinus yui* **萼部平均形态的薄板样条变形**;C. **从** *Protogloboeocrinus yini* **到** *Globoeocrinus globulus* **萼部平均形态的薄板样条变形**;D. **从** *Guizhoueocrinus yui* **到** *Sinoeocrinus lui* **萼部平均形态的薄板样条变形**。

A. Thin-plate deformations from *Globoeocrinus globulus* to *Sinoeocrinus lui*; B. from *Protogloboeocrinus yini* to *Guizhoueocrinus yui*; C. from *Protogloboeocrinus yini* to *Globoeocrinus globulus*; D. from *Guizhoueocrinus yui* to *Sinoeocrinus lui*.

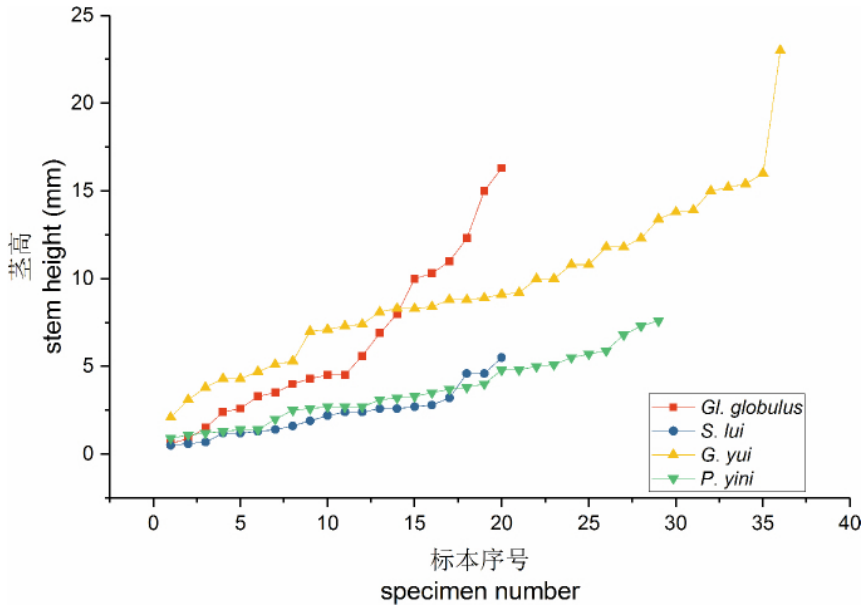

插图 8　贵州寒武系始海百合类 4 个种的茎长与萼高相关性

Relationship between thecal height and stem length for 4 Cambrian eocrinoid species in Guizhou

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5 结 论

综合 *Globoeocrinus globulus*，*Sinoeocrinus lui*，*Protogloboeocrinus yini*，*Guizhoueocrinus yui* 4 个种的萼部形态定量评价结果：1）杷榔组的 *P. yini*，*G. yui* 与凯里组的 *Gl. globulus*，*S. lui* 相比，它们的萼部大小上变化不大，大致相同；2）杷榔组的 *P. yini*，*G. yui* 在萼部形态上差别较小，均呈锥形到椭球形，而到了凯里组，*S. lui*，*Gl. globulus* 的萼部形态出现了明显的演化特征：口部区域出现了显著扩大，且在萼茎连接处出现了两极分化（变更宽或更窄）。综上，凯里组属种的萼部形态进一步发展成细长锥形或趋向于球状。萼的形态变化表明同一生态环境下寒武纪早期的 *P. yini*，*G. yui* 与中期的 *S. lui*，*Gl. globulus* 在演化上具连续性。细长的萼部配置长茎，能够更有效捕食上部水域的食物，而球状的萼部配置粗短的茎，可以增强始海百合个体的稳定性，从而适应更强的水动力环境，这种在萼部形态的趋异现象亦可能指示始海百合类在凯里组出现了生态位的明显扩张。

致谢 贵州大学资源与环境工程学院古生物地层专业博士生刘帅、文荣琴等，及当地村民刘峰、刘泽福等参加了部分野外化石标本采集工作，古生物学报审稿专家提出有益的修改意见，在此一并致以真诚的感谢。

附录 Ⅰ 形态坐标数据

Appendix Ⅰ Shape coordinates data

Taxon	标本号	X1	Y1	X2	Y2	X3	Y3	X4	Y4
Globoeocrinus globulus	GTBM-911035	464	1 698	920	1 755	912	798	561	770
	GTM-951243	680	1 928	1 283	1 813	1 010	722	575	799
	GTBM-932043	1 252	3 366	2 255	3 326	2 146	1 151	1 341	1 221
	GTBM-93007	860	4 446	1 917	4 399	1 775	2 379	963	2 416
	GTBM-952635	1 081	3 311	2 205	3 293	2 065	992	1 229	992
	GTBM-942114	807	3 613	1 937	3 586	1 715	1 241	844	1 241
	GTBM-934324	1 108	4 000	2 224	3 976	2 152	1 682	1 236	1 713
	GTBM-951740	1 589	4 980	3 056	4 616	1 980	1 695	1 038	1 924
	GTBM-951287	2 669	4 856	4 041	4 534	3 300	1 606	2 410	1 804
	GTBM-142585	1 606	5 688	3 147	5 585	2 967	1 861	1 850	1 913
	GTBM-943436	2 238	7 044	3 900	6 855	3 511	2 933	2 298	3 003
	GTBM-931147	1 264	5 723	3 039	5 723	2 618	2 002	1 537	2 013
	GTBM-93453	2 495	7 627	4 876	6 806	3 120	2 671	1 339	3 384
	GTBM-951617	1 549	8 564	3 906	8 266	3 182	3 480	1 137	3 621
	GTBM-932060	1 965	1 0336	4 737	1 0905	5 738	4 509	3 874	4 039
	GTBM-943147	1 092	3 831	1 941	3 760	1 593	1 932	960	2 037
	GTBM-921012	887	5 968	2 565	6 075	2 435	2 316	1 372	2 245
	GTBM-943341	1 130	4 298	2 981	4 486	2 834	1 348	1 642	1 244
	GTBM-953717	2 185	3 483	3 524	2 977	2 429	1 203	1 658	1 488
	GTBM-951617	2 145	5 563	3 619	5 092	2 500	1 913	1 338	2 290
Sinoeocrinus lui	GTBM-15335	881	2 335	1 462	2 243	1 065	897	783	920
	GTBM-931420	1 265	2 084	1 794	2 035	1 576	1 017	1 328	1 032
	GTBM-94001	713	1 128	1 143	1 262	1 249	489	1 046	432
	GTBM-94002	360	2 930	1 220	2 856	823	1 498	514	1 505
	GTBM-9487	772	2 903	1 609	2 867	1 260	1 412	954	1 433
	GTBM-953689	1 839	3 012	2 637	3 028	2 426	1 369	2 121	1 369
	GTBM-95001	1 391	3 342	2 359	3 342	2 062	1 608	1 711	1 616

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续表 Ⅰ

Table Ⅰ (continued)

Taxon	标本号	X1	Y1	X2	Y2	X3	Y3	X4	Y4
Sinoeocrinus lui	GTB-1531896	1 298	4 760	2 432	4 709	1 952	2 523	1 533	2 523
	GTBM-955808	1 701	3 856	2 508	3 878	2 295	2 199	1 951	2 192
	GTBM-95265	2 372	4 664	3 864	4 620	3 285	2 125	2 728	2 126
	GTBM-941154	1 556	5 285	2 887	5 193	2 360	1 977	1 793	1 990
	GTBM-943486	2 975	7 706	5 015	7 749	4 581	3 451	3 843	3 451
	GTB-161	1 230	7 314	3 114	6 943	1 948	3 164	1 102	3 266
	GTBM-931382	3 541	10 238	5 749	10 037	4 764	5 036	3 851	5 091
	GTBM-932206	1 663	10 723	4 496	10 161	2 881	5 502	1 991	5 689
	GTBM-953277	2 976	7 928	5 146	7 683	4 184	2 625	3 168	2 782
	GTBM-952688	4 174	6 687	7 332	6 412	5 898	1 240	4 754	1 369
	GTBM-95001	4 560	12 252	7 955	12 229	6 412	4 487	5 272	4 535
	GTBM-10220	3 194	14 980	6 894	14 951	6 118	6 595	4 387	6 535
	GTBM-101233B	4 254	12 156	7 589	11 939	6 212	4 253	4 810	4 422
Guizhoueocrinus yui	GZJ-2017052303	1 218	2 387	1 587	2 415	1 681	1 296	1 428	1 282
	GZJ-2017052304	2 068	4 127	2 569	4 099	2 438	1 483	2 129	1 483
	GZJ-2017052307	2 427	1 644	2 392	2 281	4 582	2 304	4 599	1 969
	GZJ-2017052309	1 714	587	1 655	1 260	5 173	1 338	5 200	1 070
	GZJ-2017052310	1 453	2 995	1 902	3 015	1 877	1 634	1 603	1 628
	GZJ-118B	1 907	2 715	2 394	2 706	2 199	1 106	1 844	1 145
	GZJ-126-103	1 825	4 507	2 438	4 594	2 648	2 459	2 273	2 394
	GZJ-126-23	814	928	773	1 672	3 848	1 488	3 860	1 183
	GZJ-37	1 187	2 511	1 494	2 506	1 436	1 531	1 254	1 536
	JLS-158-125	446	747	571	712	461	342	375	364
	KP-0-7a	1 219	1 327	1 182	1 975	4 221	1 795	4 207	1 350
	KP-3-101b	1 781	4 426	2 364	4 581	2 841	1 498	2 432	1 430
	KP-3-107a	1 758	1 258	1 647	2 039	4 734	2 344	4 801	1 989
	KP-3-142b	2 006	3 931	2 635	3 905	2 311	1 463	2 032	1 482
	KP-3-96	1 747	4 216	2 389	4 201	2 127	1 880	1 754	1 902
	KW-12-227s	2 119	2 995	2 668	3 108	2 847	1 217	2 590	1 139
	KW-12-296	1 371	3 498	1 862	3 521	1 874	1 500	1 602	1 483
	QL-106. 2	835	1 058	1 018	1 043	957	602	820	619
	QL-106. 5	1 431	2 145	1 738	2 175	1 825	1 128	1 631	1 085
	QL-111. 8	733	1 484	1 007	1 559	1 163	728	993	680
	QL-112b	1 308	2 717	1 700	2 733	1 591	991	1 373	991
	QL-115. 2a	1 262	3 180	1 668	3 180	1 556	1 341	1 273	1 347
	QL-116. 2b	1 502	3 129	1 852	3 031	1 454	1 239	1 284	1 283
	QL-126. 6	956	2 140	1 321	2 244	1 617	861	1 412	752
	QL-127-1	1 778	3 323	2 248	3 294	2 103	1 452	1 807	1 452
	QL-53. 6	830	1 753	1 078	1 753	1 033	832	860	833
	QL-54. 53	1 823	3 184	2 352	3 191	2 284	1 713	1 974	1 700

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续表 I

Table Ⅰ (continued)

Taxon	标本号	X1	Y1	X2	Y2	X3	Y3	X4	Y4
Guizhoueocrinus yui	QL-54. 5d	1 791	3 828	2 220	3 813	2 009	1 978	1 723	2 000
	QL-60b	686	1 145	892	1 108	782	597	608	636
	TG-112-115	775	1 521	1 049	1 501	962	723	744	741
	TG-112-21	897	1 368	1 112	1 376	1 102	665	935	665
	TG-112-766b	3 031	3 443	3 502	3 414	3 278	1 485	2 972	1 486
	TG-112-80	1 287	3 748	1 857	3 804	1 837	1 544	1 468	1 529
	TG-112-846	1 146	2 979	1 617	3 013	1 651	1 383	1 389	1 353
	TG-112-90	882	2 410	1 369	2 415	1 225	838	965	851
	GZJ-120	1 398	3 631	2 047	3 571	1 706	1 585	1 271	1 677
Protogloboeocrinus yini	GZJ-125-04	1 789	3 040	2 370	3 040	2 287	1 712	1 894	1 712
	GZJ-7-1205	1 431	3 740	2 203	3 766	2 190	1 866	1 720	1 866
	GJ-16-60	3 972	6 750	4 938	6 719	4 652	3 775	3 942	3 805
	GJ-126-28	3 007	5 047	3 742	5 129	3 905	2 666	3 265	2 612
	GY-266-4	2 567	5 735	3 603	5 662	3 169	2 554	2 591	2 602
	GY-266-7	2 398	5 988	3 375	6 026	3 185	2 727	2 627	2 714
	KW-2016121013	1 819	5 839	3 027	5 828	2 856	2 534	1 883	2 545
	KW-7-1005	1 905	2 149	2 493	2 214	2 526	1 066	2 172	1 017
	KW-7-145	1 708	5 157	2 627	5 145	2 412	2 566	1 816	2 579
	KW-12-215	2 324	5 063	3 443	5 265	3 694	2 680	3 134	2 536
	KW-2018011901	2 596	3 140	3 284	3 117	3 125	1 543	2 754	1 529
	KW-2018011904	4 912	4 804	5 911	4 780	5 828	2 402	5 114	2 414
	KW-2018012001	1 620	4 077	2 672	4 151	2 672	1 869	1 892	1 840
	QL-54. 5-01	2 159	3 288	2 818	3 264	2 716	1 836	2 284	1 820
	QL-545	2 112	4 081	2 913	3 962	2 577	2 089	2 090	2 122
	XX-11-103	1 826	3 878	2 838	4 398	3 718	2 194	3 085	1 900
	XX-11-105	2 705	4 607	3 797	5 137	4 489	2 920	3 796	2 584
	XX-11-148	2 235	2 710	2 783	2 755	2 800	1 445	2 370	1 418
	XX-11-162	2 802	8 166	4 442	8 341	4 490	4 043	3 518	3 963
	XX-11-164	1 882	5 716	3 276	6 181	3 907	2 882	3 038	2 596
	XX-11-172	2 636	8 178	3 442	8 783	4 824	6 191	4 248	5 817
	XX-11-197	3 458	9 804	5 107	10 123	5 567	5 035	4 556	4 840
	XX-11-214	2 432	7 340	4 322	7 261	3 925	3 511	2 527	3 543
	XX-11-216	2 758	7 609	4 084	7 368	3 000	3 692	2 125	3 917
	XX-11-26	4 129	6 404	5 117	6 657	5 554	3 783	4 922	3 645
	XX-11-283	3 078	10 233	4 554	10 180	4 414	5 345	3 394	5 327
	XX-11-305	3 816	4 013	4 696	3 951	4 448	2 167	3 828	2 167
	XX-11-306	2 271	8 192	4 065	8 166	3 639	3 586	2 632	3 638
	XX-11-72	1 750	4 998	2 852	5 078	2 727	2 624	1 989	2 601

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附录Ⅱ　传统测量数据

Appendix Ⅱ　Traditional measurement data

属种名称	标本号	萼高(mm)	萼宽(mm)	茎长(mm)
Globoeocrinus globulus	GTBM-15335	1.6	1.2	0.6
Globoeocrinus globulus	GTBM-931420	2.6	2	1.5
Globoeocrinus globulus	GTBM-94001	1.7	1.7	0.9
Globoeocrinus globulus	GTBM-94002	3.2	2.9	4.3
Globoeocrinus globulus	GTBM-9487	3.5	3.2	3.3
Globoeocrinus globulus	GTBM-953689	3.5	3.3	2.4
Globoeocrinus globulus	GTBM-95001	3.9	3.8	3.5
Globoeocrinus globulus	GTB-1531896	5	4.2	5.6
Globoeocrinus globulus	GTBM-955808	3.9	3.4	2.6
Globoeocrinus globulus	GTBM-95265	5.2	4.8	4
Globoeocrinus globulus	GTBM-941154	8	5.5	4.5
Globoeocrinus globulus	GTBM-943486	10	7.3	6.9
Globoeocrinus globulus	GTB-161	10.7	7.4	4.5
Globoeocrinus globulus	GTBM-931382	12.2	9.7	10.3
Globoeocrinus globulus	GTBM-932206	12.2	10.3	12.3
Globoeocrinus globulus	GTBM-953277	11.7	8.5	8
Globoeocrinus globulus	GTBM-952688	13.2	9.7	10
Globoeocrinus globulus	GTBM-95001	16.9	12.4	16.3
Globoeocrinus globulus	GTBM-10220	18.8	12	15
Globoeocrinus globulus	GTBM-101233B	19	12.9	11
Sinoeocrinus lui	GTBM-911035	2.458	2.8	0.6
Sinoeocrinus lui	GTM-951243	2.761	2.8	0.5
Sinoeocrinus lui	GTBM-932043	4.74	5.4	1.2
Sinoeocrinus lui	GTBM-93007	4.7	5.3	1.6
Sinoeocrinus lui	GTBM-952635	5.3	5.6	1.4
Sinoeocrinus lui	GTBM-942114	5.8	5.2	1.2
Sinoeocrinus lui	GTBM-934324	6	6.3	1.9
Sinoeocrinus lui	GTBM-951740	7.3	8.8	2.4
Sinoeocrinus lui	GTBM-951287	7.1	7.1	2.4
Sinoeocrinus lui	GTBM-142585	8.2	7.8	2.8
Sinoeocrinus lui	GTBM-943436	9.1	7.5	2.6
Sinoeocrinus lui	GTBM-931147	8.3	7.7	2.2
Sinoeocrinus lui	GTBM-93453	9.8	8.9	2.7
Sinoeocrinus lui	GTBM-951617	8.9	8.4	2.6
Sinoeocrinus lui	GTBM-932060	10.1	11.2	4.6
Sinoeocrinus lui	GTBM-943147	12.3	11.4	4.6
Sinoeocrinus lui	GTBM-921012	15.6	13.9	5.5
Sinoeocrinus lui	GTBM-943341	4.3	5.2	1.3
Sinoeocrinus lui	GTBM-953717	2.9	2.3	0.68
Sinoeocrinus lui	GTBM-951617	8.1	9.1	3.2

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续表Ⅱ

Table Ⅱ (continued)

属种名称	标本号	萼高(mm)	萼宽(mm)	茎长(mm)
Guizhoueocrinus yui	GZJ-2017052303	3.6	2.5	3.1
Guizhoueocrinus yui	GZJ-2017052304	3	2	2.1
Guizhoueocrinus yui	GZJ-2017052307	5.2	3.7	4.3
Guizhoueocrinus yui	GZJ-2017052309	8.2	5.7	8.3
Guizhoueocrinus yui	GZJ-2017052310	9.4	6.4	7
Guizhoueocrinus yui	GZJ-118B	7.6	4.7	5.3
Guizhoueocrinus yui	GZJ-126-103	8.1	6.6	7.3
Guizhoueocrinus yui	GZJ-126-23	6	3.7	5.1
Guizhoueocrinus yui	GZJ-37	7.5	3.9	7.4
Guizhoueocrinus yui	JLS-158-125	5.4	3.7	4.3
Guizhoueocrinus yui	KP-0-7a	9.2	5.1	8.8
Guizhoueocrinus yui	KP-3-101b	8.6	5.2	8.1
Guizhoueocrinus yui	KP-3-107a	5	3.5	3.8
Guizhoueocrinus yui	KP-3-142b	5.3	3.6	4.7
Guizhoueocrinus yui	KP-3-96	10.3	7.1	8.3
Guizhoueocrinus yui	KW-12-227s	12	7.5	8.4
Guizhoueocrinus yui	KW-12-296	12.9	7.7	9.2
Guizhoueocrinus yui	QL-106.2	12.9	7.3	11.8
Guizhoueocrinus yui	QL-106.5	10.6	6.8	9.1
Guizhoueocrinus yui	QL-111.8	11.5	6	10.8
Guizhoueocrinus yui	QL-112b	10.5	5.7	8.9
Guizhoueocrinus yui	QL-115.2a	10.7	6.9	10
Guizhoueocrinus yui	QL-116.2b	8.4	5.3	7.1
Guizhoueocrinus yui	QL-126.6	10.6	6.4	8.8
Guizhoueocrinus yui	QL-127-1	15	8.7	13.9
Guizhoueocrinus yui	QL-53.6	15.7	9	13.8
Guizhoueocrinus yui	QL-54.53	16.4	9.6	11.8
Guizhoueocrinus yui	QL-54.5d	16.7	8.5	12.3
Guizhoueocrinus yui	QL-60b	13.2	8	10.8
Guizhoueocrinus yui	TG-112-115	13.6	7.1	10
Guizhoueocrinus yui	TG-112-21	20.5	5.5	15.2
Guizhoueocrinus yui	TG-112-766b	24.1	11.1	23
Guizhoueocrinus yui	TG-112-80	19.3	8.8	15
Guizhoueocrinus yui	TG-112-846	21.7	8.4	15.4
Guizhoueocrinus yui	TG-112-90	21.1	9.8	13.4
Guizhoueocrinus yui	GZJ-120	23.1	11.2	16
Protogloboeocrinus yini	KW-2018011901	4.4	3.5	1.1
Protogloboeocrinus yini	KW-2018011904	4.8	4.7	2.6
Protogloboeocrinus yini	KW-2018012001	3.2	3.6	1.2
Protogloboeocrinus yini	GZJ-7-1205	4.5	3.4	2.5

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续表Ⅱ

Table Ⅱ (continued)

属种名称	标本号	萼高(mm)	萼宽(mm)	茎长(mm)
Protogloboeocrinus yini	GZJ-125-04	4.2	3.4	2.7
Protogloboeocrinus yini	GJ-16-60	3.5	2.6	0.9
Protogloboeocrinus yini	GJ-126-28	7.3	4.4	5.5
Protogloboeocrinus yini	GY-266-4	5.5	3.9	5
Protogloboeocrinus yini	GY-266-7	7.3	5.8	3.8
Protogloboeocrinus yini	KW-7-145	7.2	5.9	3.7
Protogloboeocrinus yini	KW-7-1005	5.8	4.5	4
Protogloboeocrinus yini	KW-12-215	2.6	2.7	1.3
Protogloboeocrinus yini	KW-2016121013	6.4	5.6	2.7
Protogloboeocrinus yini	QL-54.5-01	7	6.3	5.1
Protogloboeocrinus yini	QL-545	3.5	3	1.4
Protogloboeocrinus yini	XX-11-72	4.7	3.1	2.7
Protogloboeocrinus yini	XX-11-26	5.9	5	3.3
Protogloboeocrinus yini	XX-11-103	5.7	4.9	3.5
Protogloboeocrinus yini	XX-11-105	4.4	4.9	3.2
Protogloboeocrinus yini	XX-11-148	2.7	2.9	1.4
Protogloboeocrinus yini	XX-11-162	8.7	6.8	5.9
Protogloboeocrinus yini	XX-11-164	7	7.1	3.1
Protogloboeocrinus yini	XX-11-172	7.7	5.8	4.8
Protogloboeocrinus yini	XX-11-197	11.6	7.6	5.7
Protogloboeocrinus yini	XX-11-214	8.5	8.9	6.8
Protogloboeocrinus yini	XX-11-216	8.5	8.9	4.8
Protogloboeocrinus yini	XX-11-283	10.8	8	7.3
Protogloboeocrinus yini	XX-11-305	3.8	4.1	2
Protogloboeocrinus yini	XX-11-306	9.5	7	7.6

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QUANTITATIVE ASSESSMENTS AND IMPLICATIONS ON THECAL MORPHOLOGY IN CAMBRIAN EOCRINOIDS FROM GUIZHOU PROVINCE

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Key words Eocrinoids, geometric morphometrics, Balang Formation, Kaili Formation, Cambrian, Guizhou

Abstract

Eocrinoids are a representative fossil group of the Cambrian Balang biota and Kaili biota. The Balang Formation and the Kaili Formation, containing Balang biota and Kaili biota, are mainly composed of green-grey mudstone and shale. Eocrinoids, a typical ecological group in outer shelf deep-water facies, are well-preserved in large amounts in middle-upper part of the Balang Formation and the Kaili Formation. Based on measured data of thecal morphology (including landmark data and linear distances) of 105 samples among 4 species: 36 *Guizhoueocrinus yui*, 29 *Protogloboeocrinus yini*, 20 *Globoeocrinus globulus* and 20 *Sinoeocrinus lui*, we use traditional morphometric method and geometric morphometric method to investigate the morphological variation of thecal morphology of 4 eocrinoid species. The results show that little difference can be found in thecal size. Morphological variation of theca between *Protogloboeocrinus yini* and *Guizhoueocrinus yui* is relatively small, they commonly share an amygdaloidal form. However, theca shape between *Sinoeocrinus lui* and *Globoeocrinus globules* exhibits a significant variation, which indicates an evolutionary divergence: compared to eocrinoids (*Protogloboeocrinus yini* and *Guizhoueocrinus yui*) from the Balang Formation, eocrinoids (*Globoeocrinus globulus* and *Sinoeocrinus lui*) from the Kaili Formation develop a wider oral area and larger/smaller part at the bottom of the theca. In addition, in *Sinoeocrinus lui*, the theca develops a conical shape. However, in *Globoeocrinus globulus*, the theca develops a global shape. The result indicates that there is a continuous evolutionary trend in early-middle Cambrian eocrinoids. Conical theca and stem can enlarge the feeding area, while spherical thecal and short stem can make individuals adjust to stronger water energy, by attaching to the sea floor or bio-debris more tightly. This study demonstrates that there may occur an ecological niche expansion of eocrinoids in Cambrian Series 2 and Series 3.

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