

瓶筐石类化石的壁外构造及其意义^{*}

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内 容 提 要

安徽贵池—青阳地区下奥陶统红花园组的瓶筐石类化石具有非常发育的壁外构造。根据壁外构造的所在位置及其中的骨骼结构状况, 将瓶筐石类的壁外构造分成 3 大类 9 种类型, 并首次提出瓶筐石类的壁外构造具固着、加固及粘连等功能。壁外构造的发育显示了瓶筐石类与古杯类、海绵类关系密切。

关键词 瓶筐石类 古杯类 海绵动物 壁外构造 分类地位

瓶筐石 *Calathium* 是 receptaculitiid 类的一个属, 为一类海生底栖生物, 具有钙质骨骼, 广泛分布于华南早奥陶世红花园组及华北早奥陶世亮甲山组。它的生物定向、系统分类地位一直在争论之中, 是动物还是植物, 也无定论, 从它曾分别被称为“古杯海绵”、“钵海绵”、“托盘藻”便可窥豹一斑。笔者在研究安徽贵池—青阳地区红花园组的瓶筐石类 (calathiids) 标本时, 发现它们和古杯类一样, 具有清晰、发育良好、式样繁多的壁外构造 (exothecal structure)。壁外构造可帮助我们弄清 *Calathium* 的生长方向或生活位置。壁外构造以及锥状外形、具孔的钙质双壁、两壁之间有辐射状骨骼相连, 显示了瓶筐石类与古杯类、海绵动物关系密切。因而研究瓶筐石类的壁外构造对决定它们的生长方向、生物特性、生态特征和分类位置有着重要意义。

壁外构造原是用来描述古杯骨骼构造的一个术语, 系指杯体主要骨骼要素之外的次要骨骼, 它一般分布在外壁之外, 也可出现在中腔内, 甚至壁间。“壁外构造”这一术语和“枝条” (outgrowths) (Hill, 1965, 1972)、“壁外构造” (exothecal structure) 及“壁内构造” (endothecal structure) (Debrenne, 1965)、“突起” (Вырост) 及“膨起” (разрастение) (Журавлева, 1974; Журавлева и Мягкова, 1987)、“壁外组织” (exothecal tissues) (Gravestock, 1983) 等相当。壁外构造可以是实心的, 但大多数壁外构造致密且中间存有空腔或具有孔道, 空腔内的骨骼成分可以与壁间里的相同, 也可为不同的骨骼要素。这类构造在规则古杯类与不规则古杯类中都可以见到。

在瓶筐石类中也可见到与古杯类壁外构造相类似的构造, 借用古杯类的术语, 笔者也称之为壁外构造。Мягкова (1965) 在创建 *Soanites* 属时就指出该属的外壁外面有形状不定的海绵状组织 (现认为 *Soanites* 是 *Calathium* 的同义名)。之后, Журавлева 和 Мягкова (1981,

^{*} 中国科学院南京地质古生物研究所所长择优支持基金项目。

1987)又进一步强调无定形的突起是瓶筐石类的重要特性。Nitecki 和 Toomey(1979)把这类构造称之为根系(root system),郭胜哲(1983)借用古杯类的术语将这类构造称之为枝条(outgrowths),并指出中国的瓶筐石类以极其发育的枝条为特征。

在安徽贵池—青阳地区的标本中,壁外构造十分发育,大部分分布在外壁之外,也见于中腔之内,类型远远超出了 Журавлева 及 Мягкова 所讲的一种类型——无定形(amorphous)型。根据壁外构造的所在位置及其中的骨骼结构状况,我们将标本中出现的壁外构造分成 3 大类(表 I)。

表 I 瓶筐石类壁外构造的分类
Classification of the exothecal structures in the calathiids

第一大类 (Form I)	第二大类 (Form II)	第三大类 (Form III)
固着根式突起(Form I ₁) (holdfast-like process)	无定形枝条(Form II ₁) (amorphous outgrowth)	具管壁内组织(Form III ₁) (endothecal tissue with tubuli)
灰质物式突起(Form I ₂) (stereoplasm-like process)	特殊枝条(Form II ₂) (special outgrowth)	
隆起(Form I ₃) (protuberance)	似层状枝条(Form II ₃) (stratiformal outgrowth)	
	壁内枝条(Form II ₄) (endothecal outgrowth)	孔道状壁内组织(Form III ₂) (canaliculate endothecal tissue)

第一大类由致密的骨骼组织组成,可称之为突起(processes)。属于这一类的固着根式突起(型 I₁)不太多见,在一块保存很好的手标本上可见到清晰的、不规则的固着根式突起包围着一个杯体的端部并扩展到周围的基底上(见章森桂等,1991,图版 I,图 4),这一标本可与古杯类固着根的典型范例 *Tumuliolynthus tubexternus*(Vologdin)(见 Hill,1972,E8)相比拟。另有杯体以靴状或鞋跟状突起附着在其他杯体上或固着在基底上(图版 I,图 1;图版 II,图 11),在这两个杯体中突起的结构是不均一的,某些部位为实心,而另一些部位则存在空腔。郭胜哲(1983)图 5A、B 的 AC 2001 号标本及 Endo 的 *Calathium frechi*(Endo,1932, pl. 31, fig. 6)也发育有类似的突起。在一些中腔的底部(靠近杯尖的部分)可见到另一类灰质物状组织(型 I₂),这些组织致密无隙,向上迅速消失(图版 I,图 11;图版 II,图 11)。笔者认为这种组织可能是平行地沉积到内壁上的次生加厚。在许多杯体中还可见到瘤状、指状(或整齐状)或无定形状致密骨骼组织(隆起)(型 I₃)(图版 I,图 14;图版 II,图 5,10)。这种隆起的结构与外壁的结构相同,且与外壁相融合,有时可见到隆起内有孔道透过,外表面可如菜花一样,具杆状或分叉状的乳头状突起。一个杯体可同时具 2 个或更多个这样的隆起(图版 I,图 14;图版 II,图 5)。

当前的标本中,第二大类壁外组织(枝条)是最为普遍的类型,大多为无定形状及不规则状,海绵或泡沫状结构(或具弯曲状孔道)的枝条(型 II₁)。有些枝条紧紧地包围着杯体,与杯体的外壁紧密相连以至很难区分出哪是外壁,哪里是枝条(图版 II,图 1,2)。有些枝条仅从外壁的某些部位伸出(图版 II,图 4,12),也可相当大、离杯体相当远(图版 II,图 4,9)。有些枝条外表平滑,没有乳头或杆状小瘤,表面似有一薄膜盖住。在外壁与枝条之间(图版 II,图 3,6)或者两种不同的枝条之间(图版 II,图 13;图版 I,图 6)也可见到薄膜。枝

条在手标本上可反映得相当明显。

少数无定形的特殊枝条(型Ⅱ₂)也可归入第二大类中,与一般枝条(型Ⅱ₁)相比,它的空隙度更大、其中的骨骼更稀(图版Ⅰ,图8),骨骼呈骨棒状,分布无方向性,与外壁紧密相连,枝条外表裹以一薄膜。这种类型的枝条较为少见。

第二大类壁外构造还包括一些似层状枝条(型Ⅱ₃),这是一种同心状不完全地包围着杯体的枝条。多数情况下它与杯体的外壁之间存在一薄膜,但在一些部位薄膜消失,枝条与外壁相互沟通(图版Ⅰ,图6,12)。似层状枝条与一般枝条一样具海绵状或脑纹状结构,但具更多的骨骼要素及更少的空隙。从斜切面(图版Ⅰ,图12)上可看出空隙可能是穿过似层状枝条的孔道的开口,这种似层状枝条仅在杯体的一些部位出现,宽度随着个体的生长而变化(图版Ⅰ,图12)。在一个杯体中偶然见到在似层状枝条中存在一个不规则的空穴(?) (图版Ⅰ,图3),空穴中的原来结构已被重结晶所破坏,而在其它部位枝条似分成几层,推测空穴原来可能是空的或者具有同似层状枝条一样的结构,而后被破坏了。

个别情况下中腔可被与外壁之外的无定形枝条一样的枝条充填(图版Ⅰ,图8),这种壁内枝条(型Ⅱ₄)也呈具空隙的海绵状,外表具一薄膜,但它是与内壁相混,而不是与外壁;空隙度变化不定,有些部位大、有些部位小,。郭胜哲展示的图影(1983,图4B,4C,5A,5C)表明东北的标本也存在这种壁内枝条。

第三大类壁外构造是指中腔全部或部分地从底部到上部,如同许多古杯类一样,被壁外构造(壁内组织)所充填,常见的是中腔中的构造为具有管道的致密骨骼组织(具管壁内组织)(型Ⅲ₁),管道呈弯曲状或近垂直向,在横切面上为圆形、卵形或椭圆形至长椭圆形的孔(图版Ⅰ,图2,7,9,13)。管道稀密有异,随个体不同而不同。具管壁内组织常与内壁相混。在另一个杯体中可见孔道状壁内组织(型Ⅲ₂) (这种类型在安徽滁县及新疆的标本中更多见),孔道分布相当规则,孔间宽度几乎与孔径相等。这种组织也与内壁相混而不可分。

在观察具有壁外构造与不具壁外构造的标本时发现一个有趣的现象:凡是见不到壁外构造的杯体,它的中腔、尤其是壁间被各种碎屑(以生物碎屑为主)充填(图版Ⅰ,图10),这种现象说明碎屑的充填是发生在壁间(或中腔内)的软体组织腐烂之后。由此作者推测壁外构造是生物体活着时生长的,在生物体死后壁外构造就脱离了生物体或被分解了。在死去的生物体中,壁间的原生骨骼要素消失,各种生物碎屑及其他碎屑充填于壁间及中腔,多数情况下内壁及外壁可保存到最后。也有例外,即杯体的中腔内及壁间充填了许多碎屑,同时在外壁之外可见到无定形状的枝条(型Ⅱ₂),但是生有枝条的那一部分外壁之内仍是中空的,这一部分壁间未曾充填有碎屑(图版Ⅰ,图4)。此外,这个杯体的中腔的底部也可以见到具管壁内组织(型Ⅲ₁)上部散布着一些碎屑。

在各类生物中,真正发育类似瓶筐石类壁外构造的唯有古杯类。Hill(1965,1972)、Gravestock(1983)、Журавлева(1974)、Мягкова(1981)、Журавлева 和 Мягкова(1981,1987)都对古杯类的壁外构造作过详细研究,使用过各种不同的术语对壁外构造进行形态分类与描述。Hill(1972)将侧向伸出的局部或完全将杯体包围住的扩展(expansion)称为枝条,并将其分为两类:一类为从壁间伸出的,其中的骨骼要素与原来壁间的相同,又详分为细管状突起、指状突起、壁间宽度扩展、杯外突起等类型;另一类由分布在杯体基部外壁之外的致密骨骼组织构成,又可分为实心、具孔道、片状的。Gravestock(1983)又补充一种连续的成同心层

状包围杯体的带状枝条和一种柱状枝条。Журавлева 及 Мягкова(1987)将壁外构造称为扩展(разрастание)与突起(вырост),细分为 8 种类型:膜状、加厚状、无定形状、整齐状、旋圈状、管状、层状及填满中腔的。

当前标本中见到的几种壁外构造,在古杯类中几乎都可以找到与其相对应的类型。本文的型 I₁ 大略可与固着根、或 Hill 所分的第二大类(片状骨骼组织除外)相当,但 Hill 的具孔道的致密骨骼组织与实心的致密骨骼组织合并为一个类型(型 I),她的片状类型的枝条在当前标本中未曾见到过。本文的型 I₃、I₁ 及 I₂ 多少有些与 Hill 分出的细管状、指状及连续的杯外突起(杯外突起的一部分)相当。但瓶筐石类的枝条大多呈不定形,而古杯类的突起主要呈指状。瓶筐石类的壁内组织(型 II)与 Hill 指出的古杯类中腔内的枝条很相似。瓶筐石类的层状枝条与 Gravestock 描述的 *Exocyathus australis* Bedford et Bedford 及 *Somphocyathus coralloides* Taylor 的带状枝条相近。笔者所分的型 I₃、I₁ 及 I₂ 无疑与 Журавлева 和 Мягкова(1987)描述古杯类的指状与无定形状突起相似,笔者所述的具管壁内组织、似层状枝条(型 II₃)及型 I₂ 则分别与 Журавлева 等(1987)描述为管状、加厚状及填满中腔的突起相应。当前标本中有一个杯体的枝条呈螺旋状生长(图版 I, 图 2),这种生长方式与 Мягкова(1981)提出的“旋圈状”相当。

从具有壁外构造及类似的壁外构造的形态及功能类型的观点来看,笔者认为瓶筐石类与古杯类有着密切的关系,而与藻类迥然不同,因为没有在藻类及其化石中发现与壁外构造相类似构造的记载。根据文献记载,海绵有过这种类似的壁外构造,如二叠纪(Debrenne and Vacelet 1984, p. 364)及三叠纪的某些串管海绵*, Debrenne 和 Vacelet(1984)认为这种海绵的壁外构造与古杯类的壁外构造很相近。

对于古杯类壁外构造的性质、功能及分类中的意义,一直存在着很不相同的看法。Вологдин、Bedford 等认为有一些壁外构造是独立的古杯属种(Hill, 1972)。为此,Вологдин 在 1931 年建立了迷形古杯属(*Labyrinthomorpha*), 1962 年又建立了小整洁古杯属(*Tersiella*), Bedford(1937)创立了外古杯属(*Exocyathus*)及近形古杯属(*Metaldetiomorpha*),用以代表一定形态的壁外构造。另一些古杯专家则看法不同,他们认为壁外构造是古杯体不可分割的组成部分,或起固着、加固及粘连的作用,或是无性生殖的一种方式(一个杯体通过指状枝条生出“新芽”而变成一个复体)。Журавлева(1974)甚至认为壁外构造是同种异形(雌雄异形)的表现形式。也有人认为一些壁外构造可能是不具内壁或中腔的包壳状古杯。也有持其他意见的,如认为大部分壁外构造是其他生物(包壳生物、吸附或寄生物,如藻类、层孔虫类)所产生的骨骼或组织。时下流行的看法是认为壁外构造是古杯体的一部分,起固着、加固及粘连的作用。笔者赞同这一意见,认为瓶筐石类的壁外构造是瓶筐石类杯体分泌而成的骨骼组织,而不是其他生物包裹或寄生在瓶筐石类杯体上时生成的。我们的材料中有 2 个标本(图版 I, 图 7, 9)是这种解释的很好例证,这 2 个杯体的壁外构造的组织与杯体的外壁密切不可分,很难在它们之间划出一条界线。其次,笔者还认为瓶筐石类的壁外

• 周又敏、韩乃仁(1990)在《钝管海绵硅化标本的研究》(广西地质, 3 卷 1 期)中称这类构造为赘生物(modes or knots)

构造与古杯类的壁外构造一样也有固着、加固及粘连等功能。固着根式突起(型 I₁)与灰质物式突起(型 I₂)分布在杯体的基部及中腔的底部,对杯体固着在基底或其他杯体上起着重要作用;固着根式突起扩大了杯体与基底(或其他的杯体)的接触面,增强了固着的强度,因此这类突起具有良好的固着作用;灰质物式突起增加了杯体的重量,降低了重心,增加了杯体在水流或波浪中的稳定性,这种突起同时起着加固作用。突起(型 I₂)从外表上看可能与鹦鹉螺类的内体管式沉积较为相似。第二类壁外构造(型 II)(无定形枝条及其他枝条)推测主要起粘连作用,无定形枝条将杯体与其他生物体(藻类、疑难藻类、棘皮动物、苔藓虫、层孔虫、海绵等)连接起来,在枝条的连接下(图版 I,图 13),这几种生物相互依靠、相互支持,增强了生物体的稳定性,形成了一种群居生长的方式。北美古生物学者显示的清晰图片(Nitecki and Toomey, 1979, figs. 51, 67)说明那里的瓶筐石类的壁外构造也具粘连功能。笔者推测这种枝条可能只在某种特别适合于瓶筐石类及其它一些具群居生活习性的生物,如藻类、疑难藻类、棘皮动物、海绵等生存与发展的环境中出现,在这种环境中这些生物相当密集,甚至形成生物丘或礁。一个可能的例子就是 Alberstadt 和 Walker(1976)报道的北美田纳西州中奥陶世 Elk 河礁的葵盘石-棘皮动物先驱群落中的瓶筐石类具一“钙化强烈”的外层,外层无定形,海绵状、有孔(?) (他们将这种外层构造看作是在瓶筐石类中从未报道过的一种特征,这种构造实际上就是我们所称的壁外构造)。笔者所看到的另一个类似例子是我国长江三峡地区早寒武世的古杯类,原古杯(*Archaeocyathus*)具极其发育的壁外构造,它将许多杯体和一些藻类(或疑难藻类)连接在一起,形成古杯-藻类生物礁。第三类壁外构造(型 III)推测也是起着加固杯体的作用,使杯体更能经受住波浪、潮汐或水流的冲击,增加杯体的稳定性。

对于瓶筐石类来说,壁内组织与枝条可能如郭胜哲(1983)所述,壁间的软体组织透过内、外壁孔分别进入中腔或外壁之外,分泌出填充在中腔内的壁内组织及枝条,或包围外壁的壁外枝条。

瓶筐石类是一类已绝灭的底栖海洋生物,并被认作是葵盘石类 receptaculitids 的一部分。这类生物的生长和定向,近几十年来一直是激烈争论的问题,正如 Fisher 和 Nitecki(1982)所述:“葵盘石类的生长和方向一直是近期研究的中心,但这又是更老的问题——如何确定葵盘石类的生物亲缘关系这一问题的基础。”将葵盘石类归于海绵的研究者认为生物体成各种锥状,具穴的一端显然朝上,封闭端(杯尖)在最下面,瓶筐石类的杯体以杯尖及一些壁外构造固着在基底上。Nitecki 及其他持藻类观点的研究者则对瓶筐石的生长方向有不同的见解,他们认为杯尖(封闭端)朝上。这样,生物体的生长方向便与生物亲缘关系密切相关;如果生物体被看成是藻类,那么杯尖便朝下;反之,认为杯尖朝下的人也就不认为生物体是藻类,而是海绵或其他动物(或者是独立的已绝灭的门类)。

当前材料对非藻类说是个有力的证据。有些杯体具有明显起固着作用的固着根式突起,突起围绕着杯体的下部,很难设想这些钙质突起会处在生物体的顶端。固着根式突起是一种示底组构;同固着根式突起一样,灰质物式突起也是一种示底组构。这些示底组构表明在生长期间杯尖显然是朝下的,而空端是朝上的。再一个例证就是图版 I 图 4 所示的标本,它的中腔下部可见到壁外构造,其上稀疏地分布着一些生物碎片和其他碎屑,隔着几块较大的碎片,上面密集地分布着各种生物碎屑。与此同时,这个杯体的壁间的中上部被各种碎屑(主要

是生物碎屑)充填,但下部(靠近杯尖的部分)近于中空,没有碎屑。在杯体生长与生活期间充满具有生命的软体组织,碎屑不可能充填到壁间;只有在生物死亡、软体腐烂之后碎屑才能充入,而且只有在杯口朝上时各种碎屑才可能以这种形式充入到中空与壁间。如在杯口朝下或杯体横卧的情况下,生物碎屑及其他碎屑在中腔及壁间都不大可能形成这种形式的充填。

另外,在图版 I 图 5,图版 II 图 3 所示的标本中可见到杯体的壁间上口似有一膜状物存在,膜将外界与壁间隔开,同时也可看到这两个杯体的中腔都存在无定形型枝条,枝条从中腔沿壁间上口的膜向外生长,直至围着杯体的外壁发育。枝条的这种生长方式也只有杯口朝上的情况下才会发生,如是杯口朝下与基底相接触,那么壁间上口不可能出现这样生长的枝条。

当前材料充分证明了瓶筐石类在生活时应为杯口朝上、杯尖在下的生长方式。这些标本显示的瓶筐石类的生长方式是古杯类、海绵类一致。瓶筐石类与古杯类的生长方式之间的相似性显示出瓶筐石类、尤其是中国及西伯利亚的瓶筐石类与古杯类的密切关系。此外,瓶筐石类与古杯类之间还存在一些其它的相似性:锥状外形,清楚的具孔的双壁,两壁之间具辐射状骨骼要素,具各种壁外构造,中腔可能中空,骨骼要素钙化均一,两壁的孔或孔管构成滤食系统,相同的生长方向、固着方式及生活习性等,所有这些都证明瓶筐石类与古杯类之间有着密切的关系。

安徽省地矿局 324 地质队李昌文、叶何青、何建平等协同笔者采集标本,中国科学院南京地质古生物研究所蒋汉培磨制薄片,研究工作中得到中国科学院地质研究所范嘉松的帮助,笔者在此一并诚表谢意。

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[1995年5月23日收到]

EXOTHECAL STRUCTURES OF THE CALATHIIDS AND THEIR SIGNIFICANCE

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Key words calathiids, archaeocyathids, sponges, exothecal structure, taxonomic position

Summary

Calathiids i. e. calathiid receptaculitids are a group of enigmatical organisms. The problems of their nature, life orientation and taxonomic position have been argued for the recent 20—30 years. They have been “interpreted by various authors as calcareous algae, pine cones, foraminifers, sponges, corals, cystoids, tunicates, …… transitional forms be-

tween sponges and corals, or an independent extinct phylum……. "Some palaeontologists consider them as sponges (animals), while others as algae (plants). Investigators with sponge interpretation believed that due to the calathiids in growth position with the open apertural end obviously orientated upward and the closed end (pointed apex of cup) at the lowermost, the organisms were variously conical in form, those with algal interpretation commented in opposite way on the orientation of calathiids, and deduced the apex (closed end) to be orientated upward. People holding different opinions have a lot of strong, individual arguments; such a dispute about the nature and orientation of calathiids is still continued up to now.

In the calathiid specimens from S. Anhui on hand, the author discovered remarkable, well-developed and various exothecal structures, which are often similar in appearance to those in fossil archaeocyathids. Researches on the exothecal structures of calathiids have profound significance helpful for determining their life orientation, biological nature, ecological features and taxonomy. The holdfast-like stereoplasm surrounding the exterior and adjacent area of the lower part of a cup serves as an excellent example. This and other material with exothecal structures may make clear the growth or life position of calathiid receptaculitids, in which the apex with holdfast-like structures has been orientated downward. The conical forms, porous calcareous double walls, radial skeletons in contact with both walls and exothecal structures indicate that the calathiids are related to archaeocyathids and sponges, and differ obviously from algae.

The exothecal structure is a term used in the skeletal structure of Archaeocyatha. In the author's mind, it means the supplementary skeletal elements, except the primary skeleton of the cup, external outer wall and in central cavity, even in intervallum. The exothecal structure may be dense tissue without spaces or canals, or dense tissue with spaces or pierced by canals for the most part. In the spaces of the exothecal structure, skeletal elements may be the repetitions of intervallum skeletal elements or those distinct from the elements. Such exothecal structures have been observed in both groups, regular and irregular archaeocythans.

In calathiid receptaculitids, the structures similar to exothecal structures of archaeocyathans were also reported. The author calls the structures exothecal structure after Archaeocyatha. While erecting the new genus—*Soanites*, Myagkova (1965) pointed out that there was amorphous sponge-like tissue beyond the outer wall of the genus. This was the first formal record. Then Myagkova (1981), Zhuravleva and Myagkova (1987) again stressed that the amorphous processes are the important characteristic of calathiid receptaculitids. Toomey and Nitecki (1979) called such a structure the root system.

Guo Sheng-zhe (1983) called the structures the outgrowth and pointed out the calathiid specimens of China characterized by well-developed outgrowths. His discussion touched on the morphology, distribution, function and origin of the outgrowths.

In our material from S. Anhui, the exothecal structures occur in the cavity and beyond the outer wall of the cup. Their forms are more than one (amorphous) as pointed by Zhuravleva and Myagkova. According to their position and skeletal elements, the exothecal structures of our material may be grouped into three categories:

The first category consists of dense skeletal tissue (process). The holdfast-like process (Form I₁), which was found in two cups, belongs to the category. On a well-preserved hand specimen, the remarkable and irregular holdfast-like process is surrounded by the exterior of the lower part of the cup and is expanding over the substratum (see Zhang Sen-gui *et al.*, 1991 pl. I, fig. 1). The wonderful circumstance may be compared with the outstanding example of the holdfast in *Tumuliolynthus tubexternus* (Vologdin) under Archaeocyatha, as discovered by Zhuravleva (1949). One cup is found to be attached on another with a pedestal or heel holdfast-like process (pl. I fig. 1). Similar situation is also seen in Archaeocyatha. Vologdin (1962) reported in *Loculicyathus salairicus* Vologdin holdfast formed of dense skeletal tissue. The structures of processes (Form I₁) in the two calathiid cups are not uniform; in one area they are massive without spaces and in the other area they are massive with spaces. The specimen AC2001 of Guo (1983, Fig. 5B) and Endo's *Calathium frechi* (Endo, 1932, pl. 31, fig. 6) developed similar processes (which Guo called the root-like process). At the bottom of the central cavities in certain cups may be found another kind of stereoplasm-like tissue (Form I₂) which is dense without spaces and rapidly disappears upward (pl. I, fig. 11; pl. I, fig. 11). The texture of the tissue has been destroyed recrystallization. The author considers the tissue (Form I₂) as secondary thickening deposited parallel to the inner wall. Nodular, fingered (tersioid) or amorphous dense skeletal tissues, i. e. protuberances (Form I₃) are shown in many cups (pl. I, fig. 14; pl. I, figs. 5, 10). The texture of the protuberances is the same as that of the outer wall while the protuberances are fixed with the outer wall and sometimes may be pierced by canals, or possess rhabditiform and bifurcated mammillae on the outer surface (pl. I, fig. 14; pl. I, figs. 5, 10). Two or more such protuberances may occur simultaneously in a cup (pl. I, fig. 14; pl. I, fig. 5, 10).

The second category of skeletal tissue (outgrowth) is the common exothecal structure in our specimens. The outgrowths are amorphous and irregular tissue with spongy or vesicular texture or with complicated meandroid canal-like spaces (Form I₁) in majority. Some outgrowths (Form I₁) closely encircle the cups and link up the outer walls until it is difficult to distinguish the outer wall from the outgrowths (pl. I, figs. 2, 4). Some amorphous outgrowths expanding from a limited area of the outer wall (pl. I, figs. 4, 12) may be fairly large and considerably far apart from the cup (pl. I, figs. 4, 9). In some outgrowths a pellicle is developed over the smooth outer surface, without mammillae or rhopaloid nodules. The pellicle is also found between the outer wall and the outgrowths (pl. I, figs. 3, 6), or between two kinds of different outgrowths (pl. I, fig. 6; pl. I, fig. 13). On the hand

specimen are obviously displayed the outgrowths (Form I₁).

This category may contain a few amorphous special outgrowths (Form I₂) with more meandroid canal-like spaces and less skeletal elements than the outgrowths as stated above (pl. I, fig. 8). The skeletons in the special outgrowths (Form I₂) are rod-like and disorderly in arrangement. These outgrowths also closely link up the outer wall and are encrusted by a pellicle. However, this type is rare.

This category also includes stratiform outgrowths (Form I₃) which concentrically and incompletely surround the cup. A pellicle is developed in most part of the contact face between the outer wall and the outgrowth, and disappears in a limited area of the face, then the outer wall and the outgrowth fix together. The stratiform tissue with spongy or vesicular texture is similar to the outgrowth (Form I₂), but with more skeletal elements and less spaces than the latter. The spaces may be the opening of canals perforating through the stratiform tissue on the oblique section. It is observed (pl. I, fig. 12) that such stratiform tissue may appear only in a limited area of the cup, and its width may vary during growth. Occasionally an irregular cavity (?) is found in a cup with stratiform outgrowths (pl. I, fig. 3). In a limited area the stratiform outgrowths of the cup may be divided into some zones. The primary structure of the cavity has been destroyed by recrystallization. It is assumed that the original cavity (?) was empty or with the same texture as the stratiform tissue, which disintegrated afterwards.

More rarely the central cavity may be full of amorphous outgrowths just like those beyond the outer wall (Form I₂) (pl. I, fig. 8). The endothelial outgrowths (Form I₄) are also spongy with more or less spaces, and possess a pellicle on outer surface, but they fuse with the inner wall, instead of with the outer wall. The space coefficient varies within a considerably wide scope, in some areas on the small side, and in other areas on the large side, while in a limited area the tissue is lost. The figures of Guo (1983, figs. 4B, 4C, 5A, 5B) indicate that these endothelial outgrowths appear in the specimens of NE China.

The third category consists of the central cavity wholly or partially filled with the exothecal structure (endothelial tissue) from base to upper part, just like those of many archaocyathans. The structure in the cavity may be dense skeletal tissue pierced by tubuli (Form III₁), which are bent or subvertical, and rounded or oval, or elliptical and elongated elliptical opening in transversal section (pl. I, figs. 2, 7, 9, 13). The tubuli may crowd in some cups and scatter in others, with more spaces in cavities. The endothelial tissue with tubuli is fixed with the inner wall. In another cup the cavity may be brimful with canalliculate endothelial tissue (as commonly seen in the calathiid specimens from Chuxian of Anhui, and Xinjiang). The tissue canals are fairly regularly arranged and the intercanals are almost as wide as the canals. The tissue is also fixed with the inner wall.

In observation on our specimens with and without exothecal structures, the author discovered an interesting phenomenon that in the cups without exothecal structures, there are

various clastics mainly composed of bioclasts, stuffed in central cavities especially in the intervallum. (pl. I fig. 10). This phenomenon indicates that the filling of clastics should take place after the corruption of the soft part in the intervallum (or central cavity). Judging from this phenomenon, the author imagines that the exothecal structures might have grown in the living organisms; after the death of the organisms, the exothecal tissues might be free or have been destroyed. In the dead organisms, the primary skeletal elements within the intervallum disappeared, with various bioclasts and other clastics filling in the intervallum and the central cavity. Eventually, in the dead organism the outer and inner walls might be mostly preserved. The sole exception (pl. I, fig. 4) is a cup with amorphous outgrowth (Form II₁) beyond the outer wall. The central cavity and the intervallum are filled with various clastics, but the area of the intervallum, in touch with the limited area of the outer wall with outgrowth, is empty and free of clastics. Besides, in the cup the endothecal tissue with tubuli (Form III₁) is discovered only in the lower part of the central cavity, with a few scattered clastics distributed over the upper part.

In various organisms only Archaeocyatha developed such a kind of similar exothecal structures. Hill (1965, 1972), Gravestock (1983), Zhuravleva (1974), Myagkova (1981), Zhuravleva and Myagkova (1981, 1987) examined and discussed in great detail the exothecal structures of archaeocyathans with various terms, and classified them based on morphology. Hill named lateral expansions affecting a sector or the whole circumference of the archaeocyathan outgrowths and divided them into two groups. Group I consists of expansions from the intervallum in which the skeletal elements are usually similar to those in the original intervallum, including (1) the slender, tubular process type; (2) the tersiae, or tersioid process type; (3) the intervallar expansion (in width) type and (4) the exocyathoid expansion type. Group II is composed of dense skeletal tissue beyond the outer wall, and may be distinguished into (1) dense skeletal tissue without canals or spaces; (2) dense skeletal tissue pierced by canals and (3) dense skeletal tissue with laminae. The holdfast and the septate (and tabulate) structures, tubulose and canaliculate tissue are actually contained in the outgrowths (Hill, 1972, fig. 6, E 21). Gravestock (1983) added a continuous concentric zoned buttresses and a pillar buttresses to the outgrowths. Zhuravleva and Myagkova (1987) called the exothecal structures the expansions (разрастение) and process (вырост). They subdivided the expansions and processes into 8 types: (1) glume; (2) crassus; (3) amorphous; (4) tersioid; (5) gyrata; (6) tubuli; (7) stratum and (8) full central cavity.

Some forms of the exothecal structures in our material stated above may be separately found and roughly corresponding to the types of exothecal structures in archaeocyathans. Our Form I₁ is approximately comparable with the holdfast, or Hill's Group II (except for the laminate skeletal tissue). But Hill's dense skeletal tissue pierced by canals and dense skeletal tissue without canals or spaces are induced into one form (our Form I₁) in

taxonomy, and her laminate dense skeletal tissue has not been discovered in our specimens. Our Forms I₃, II₁ and II₂ look more or less similar to those of the slender, tubular processes, tersioid processes and continuous exocyathoid expansions (partially exocyathoid expansions) of Hill. But in our specimens, the outgrowths are mostly amorphous, and the processes of archaeocyathans are mainly tersioid. Our endothecal tissues (Form III) are fairly similar to the outgrowths in the central cavity of archaeocyathans raised by Hill. The stratiformal outgrowths in our specimens resemble the zoned buttresses in *Exocyathus australis* Bedford et Bedford and *Somphocyathus coralloides* Taylor, as stated by Gravestock. Our Forms I₃, II₁ and II₂ are undoubtedly analogous to the tersioid and amorphous processes of Zhuravleva and Myagkova (1987). Our endothecal tissues with tubuli, stratiformal outgrowths and Form I₂ may be separately equivalent to their tubuli, crassus and full central cavity. The outgrowth in a cup (pl. I, fig. 12) shows a spiral growth; its growth pattern may be equivalent to the gyrata advanced by Myagkova (1981).

From the viewpoints on exothecal structures and similar morphological and functional types the author believes that the calathiids were closely related to archeocyathan and distinguished from the algae, for no any record of the similar exothecal structures has been found in living and fossil algae. According to literature there are similar exothecal structures in sponges, such as certain sphinctozoans of the Triassic (Debrenne and Vacelet, 1984, p. 364). Debrenne and Vacelet considered this type of exothecal structures as very close to that in archaeocyathans. The exothecal structures of archaeocyathans continue to provoke discussion with respect to their structure, nature, function and taxonomic significance. Several scholars, such as Vologdin, Bedford and Bedford, considered some of these exothecal structures as not dependent upon certain archaeocyathans; for example, *Coscinocyathina*, and *Archaeosycon* are all taxa. Vologdin erected *Labyrinthomorpha*, *Tersia* in 1931 and *Tersiella* in 1962, while Bedford and Bedford (1937) established *Exocyathus* and *Metaldetimorpha*. However, other investigators on archaeocyathans thought quite differently. They believed that the exothecal structures were an integral part of the whole archaeocyathid organism, and appeared to have anchoring, reinforcing and adherent functions or to be in a way of asexual reproduction (with 2 cups through the tersioid outgrowths bearing other young cup "buds" to form a colony). Zhuravleva (1974) even regarded the exothecal structures as a manifestation of dimorphism. Someone deemed that several structures might encrust the archaeocyathans without inner wall or central cavity. Opposite to the above viewpoints, some scholars considered most of the exothecal structures as tissues or skeletons borne by other living organisms (crusting organisms, parasites or adsorbing organisms, such as algae, stromatoporoids). Since the exothecal structure is part of the archaeocyathid body, the anchoring, reinforcing and adherent function interpretation still holds a dominant position and the author also subscribes to the opinion.

At the same time, the author also considers the exothecal structures as skeletal tissues

secreted by the calathiid cups, instead of formations encrusted or parasitized by other organisms. Two cups in our specimens (pl. I, figs. 7, 9) enable well clarification of this interpretation. The exothecal structures of the cups are so closely combined with the outer wall that it is difficult to draw a clear demarcation line between them. Moreover the author also considers that the exothecal structures of calathiids might possess the same functions as those of archaeocyathans, including anchoring, reinforcing and adhering. The holdfast-like processes (Form I₁) and the stereoplasm-like tissues (Form I₂) surrounding the base of the cups and filling in the lower part of the central cavity, might play an important role in anchoring on the substratum or other cups. The processes enlarge the touch-face between the cup and the substratum (or other cups), and strengthen the attaching force. For this reason the processes possess an anchoring function. The stereoplasm-like tissues increased the weight of the cup with the centre of gravity lowered and the stability in water current or wave greatly improved. The tissues were consistent with a reinforcing function. However, the protuberances (Form I₃) may rather resemble the intracameral deposits of nautiloids in appearance. It is very reasonable to assume that the second category of the exothecal structures (the amorphous and other outgrowths) were mainly effective for adherence. The amorphous outgrowths combined the cup with other calathiid cups or other organisms (algae, problematic algae, echinoderms, ? bryozoans, stromatoporoids). In the action of the outgrowths (pl. II, fig. 13) some kind of organisms both depended on and supported each other, forming a more firmly stabilized and gregarious style of growth. There are good figures for us to believe that the calathiids of North America possess exothecal outgrowths with adherent function (Toomey and Nitecki, 1979, figs. 51, 67). Furthermore, the author infers that this kind of outgrowth may appear only in certain circumstances suitable for existence and growth of calathiids and other organisms with gregarious growth characteristics, such as algae, problematic algae, echinoderms, poriferans and so on; these organisms must be fairly crowded, and even may be transformed into bioherm or reef.

A possible example is the calathiids in a receptaculitid-echinoderm pioneer community of the Middle Ordovician Elk River Reef in Tennessee (North America), with "a heavily calcified outer layer" showing an amorphous sponge-like porous ? appearance as reported by Alberstadt and Walker (1976) (who regarded the structures as a feature which has not been previously described in calathiids; such structures are actually just what we call the exothecal structure). Another example observed by the author is the well-developed similar exothecal structures of *Archaeocyathus* in the Lower Cambrian archaeocyathid-algae reef of the Yangtze Gorge. There many cups and some algae (or problematic algae) combined together through the exothecal structures. The author believes that the endothecal tissue also may play a reinforcing role and increase the stability of organisms to experience the pounding of sea waves, sea tides or ocean currents.

Some endothelial tissues in the central cavity of archaeocyathans, such as *Robustocyathus robustus* (Vologdin) and *Ajaciccyathus demboi* Vologdin, are interpreted by Vologdin as calcified soft parts. Holding a different opinion from Vologdin, Zhuravleva regarded them as being formed by the extrusion of a soft tissue into the central cavity from the intervallum, and this soft tissue then proceeded to secrete skeletal elements; Maslov (1960) advanced that the tissues were deposited by a second, single-walled archaeocyathan in symbiosis with the first one. With objection to Vologdin and Zhuravleva's interpretations, Fonin (1961) was unconvinced of the existence of an "internal digestive organ" in the central cavity, and could not accept that this organ was normally empty during the life of the individual. Hill (1972) felt that Zhuravleva's explanation seemed to be the better one. For the endothelial tissue and outgrowth of calathiids, the structures might be secreted by the soft tissue expanded through the pores of the inner wall, as mentioned by Guo (1983). The author agrees with Guo's view, that the soft tissue in the intervallum seemed to have extruded through the pores in the outer and inner walls separately into the central cavity and the exterior of the outer wall, and secreted the exothecal outgrowths surrounding the outer wall and also the endothelial tissue and outgrowths filled in the central cavity. As a group of extinct, sessile marine organisms, calathiids have been considered as part of receptaculitids. Their growth and orientation have been a heatedly argued problem in the last decades, just like what Fisher and Nitecki (1982) pointed out: "Receptaculitid growth and orientation have been the explicit focus of a number of recent studies (e. g., Gould and Katz, 1975), but they also underlie the much older problem of determining the biological affinities of receptaculitids." Various authors, who interpreted them as sponges, believed that the calathiids in growth position with the open apertural end obviously orientated upward and the closed end (pointed apex of cup) at the lowermost, were variously conical in form. The calathiid cups fixed on the substratum with the closed end and some of the exothecal structures. Nitecki (1962) and others with algal interpretation commented in opposite way on the orientation of calathiid growth, and deduced the apex (closed end) to be orientated upward. Thus the orientation of organisms is closely related to biological affinities. If the organism is regarded as algae, the apex (closed end) must be orientated upward; if it is regarded as sponges, the apex must be orientated downward. On the contrary, if someone regarded the closed end as orientated upward, the organism must be interpreted as algae; if others regarded the closed end as orientated downward, the organism must be interpreted as non-algae (sponges or some other animals, or an independent extinct phylum). Since 1978 Fisher and Nitecki (1978, 1982) inverted their orientation, they regarded the closed end as the fixing part on the substratum and continued to believe the organisms belonging to algae. They commented the issue of polarity upon the addition of new elements. For this phase, they were not concerned about which end of a receptaculitid was oldest or youngest, or about which end was located lowermost or uppermost. In many re-

ceptaculitids, such as some British specimens of *Ischadites koenigii* (Fisher and Nitecki, 1982, Text-fig. 1c), *Receptaculites biconstrictus* (Fisher and Nitecki, 1982, Text-fig. 1k) and *Selenoides iowensis* (Fisher and Nitecki, 1982, Text-fig. 11), they called the closed end the nucle and the open foramen the lacunae. Thus the mind about the orientation of calathiids (even whole receptaculitid) seems to be identical, but the biological affinities have been a problem in dispute.

Our material is a strong evidence for non-algae interpretation. In two cups (pl. I, fig. 1) the holdfast-like processes, which remarkably play an anchoring role, must be surrounded by the lower part of the cup. It is too ghastly to contemplate that the calcareous process could be situated at the top of the organism. Just like the holdfast-like process, the stereoplasm-like process also may be one of the geopetal fabrics. These geopetal fabrics indicate that during the growth the apex of the cup was obviously orientated downward and the open end upward.

In the specimen (pl. I, fig. 4) mentioned in the preceding chapter, exothecal structures are developed in the lower part of the central cavity, with the upper part of the central cavity partitioned by a few large clastics into two parts. Different calcareous clastics, mainly bioclasts, are scatteredly distributed over the lower part, and crowdedly distributed in the upper part. At the same time the middle and upper parts of the intervallum in the cup are also permeated with different clastics (mainly bioclasts), while the lower part (near the apex of the cup) seems to be empty and free of clastics. During growth and life of the cup the intervallum is occupied by the living soft tissue, and very unlikely by the clastics. The filling with clastics must be after the death of the cup, and must happen in case of a life position with aperture upward. Only in this case can the clastics fill in the gaps in the intervallum and the central cavity in this kind of mode. In case of a life position with aperture downward or in horizontal growth the mode of filling with bioclasts and lithoclasts in the intervallum and the central cavity would be different from the mode as stated above. In some specimens (pl. I, fig. 5; pl. II, fig. 3) a pellicle, which seems to happen in the ostia at top of the intervallum, separates the intervallum from the surroundings and the amorphous outgrowths in the central cavities of the cups, following the pellicle from the central cavity until apart from the outer wall. The mode of outgrowths must appear just under the circumstances of a life position with the aperture upward instead of under the circumstances with the aperture orientated downward and attached on the substratum.

Our materials have been an eloquent proof of their growth orientation and life position, in which the calathiid cups were situated in a position with the open apertural end at the top of the body and the pointed apex in the lowermost part. The mode of calathiid growth as indicated by our specimens is the same as that of archaeocyathans, and sponges. The similarities in the mode of growth between calathiids and archaeocyathans indicate a close relationship between calathiids, especially Chinese and Siberian calathiids, and ar-

chaecocyathans. Moreover, between calathiids and archaeocyathans there are some other similarities, including conical shapes, distinct porous double walls, radial skeletal elements between both walls, various exothecal structures, possibly empty central cavity, uniform calcification of skeletal elements, presence of current canals (or pores) in both walls constructing a filtration system, orientation of growth, mode of attachment, living habit and others. All these prove the close relationship between calathiids and archaeocyathans.

图 版 说 明

标本全部保存在中国科学院南京地质古生物研究所,均产于下奥陶统红花园组。除注明者外,都采自安徽青阳五溪马家岭。

图 版 I

1. 纵切面,示一个杯体通过固着根式突起(型 I₁)固定在另一个杯体上,×1.8。
- 2,13. 示中腔内的具管壁内组织(型 II₁),×3.2. 横切面;13. 纵切面。
3. 横切面,示杯体具层状枝条(型 I₃),枝条中具一空穴,×1.2。
4. 纵切面,示中腔及壁间内部分被碎屑充填,×1.2。
5. 斜纵切面,示壁外组织从中腔中一直伸到体外,×1.2。
6. 斜横切面,示不同杯体的壁外构造被薄膜隔开,×1.8。
- 7,9. 示中腔内的具管壁内组织(型 II₁)。7. 斜纵切面,×1.8;9. 横切面,×3。
8. 斜切面,示特殊枝条(型 I₂),×2。
10. 横切面,示碎屑充满了中腔及壁间,见不到壁外构造,×0.6。
11. 斜纵切面,示中腔内具灰质物式突起(型 I₂),向上很快尖灭,×1.2。
12. 横切面,示枝条似成螺旋状生长,两层枝条间有薄膜隔开,×1.8。
14. 横切面,示外壁外具多个隆起(型 I₃),隆起与杯体外壁界线不明,×1.8。

图 版 II

1. 斜横切面,示杯体具无定形状枝条(型 I₁),×1.8。贵池桃坡老屋里。
2. 横切面,示杯体具枝条(型 I₁),似呈辐射状,×1.8。
3. 斜纵切面,示壁间上口存在膜状物,壁外组织沿膜向外生长,×1.2。
4. 斜切面,示枝条(型 I₁)向外伸展相当远,×1.8。
5. 纵切面,示杯体具多个隆起(型 I₃),隆起端部呈菜花状,×1.2。
6. 横切面,示杯体具层状枝条(型 I₂),×1.2。
7. 弦切面,示杯体的外壁逐渐变成枝条,×2。
8. 纵切面,示中腔内的壁内枝条(型 I₄),×1.2。
9. 弦切面,示杯体的外壁向外演变为枝条,枝条向外扩展相当远,×2。
10. 横切面,示外壁外具多个隆起(型 I₃),隆起与杯体外壁界线不明,×1.8。
11. 纵切面,示中腔内具灰质物式突起(型 I₂),壁外具固着根式突起(型 I₁),×2。贵池桃坡老屋里。
12. 斜纵切面,示杯体外的似层状枝条(型 I₃),枝条仅在杯体的一定部位存在,×2。
13. 斜切面,示壁外构造的粘结作用,×3。

