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# Cambrian stalked echinoderms show unexpected plasticity of arm construction

**S. Zamora* and A. B. Smith**

*Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK*

Feeding arms carrying coelomic extensions of the theca are thought to be unique to crinoids among stemmed echinoderms. However, a new two-armed echinoderm from the earliest Middle Cambrian of Spain displays a highly unexpected morphology. X-ray microtomographic analysis of its arms shows they are polyplated in their proximal part with a dorsal series of uniserial elements enclosing a large coelomic lumen. Distally, the arm transforms into the more standard biserial structure of a blastozoan brachiole. Phylogenetic analysis demonstrates that this taxon lies basal to rhombiferans as sister-group to pleurocystitid and glyptocystitid blastozoans, drawing those clades deep into the Cambrian. We demonstrate that Cambrian echinoderms show surprising variability in the way their appendages are constructed, and that the appendages of at least some blastozoans arose as direct outgrowths of the body in much the same way as the arms of crinoids.

**Keywords:** echinoderms; Cambrian; X-ray tomography; evolution; phylogeny

## 1. INTRODUCTION

Understanding the origin of metazoan body plans continues to pose one of the great challenges for palaeobiologists. While knowledge of the molecular basis underpinning the Cambrian explosion has been the major focus of attention recently (e.g. [1,2]), palaeontology continues to play a key role in providing the empirical patterns of phenotypic change that molecular genetics seeks to explain (e.g. [3]). Analysis of this record has recently highlighted several important features of the Cambrian explosion: the high plasticity of form that is encountered in the early stages of diversification [4], the unexceptional levels of morphological disparity being generated [5] and the considerable detail in which the assembly of body plans can be reconstructed from the Cambrian record for some groups [6]. Echinoderms provide an unrivalled opportunity to examine body plan evolution during the Cambrian. Not only do they have a complex multiplated skeleton that allows robust phylogenies to be constructed, but they have also diverged more markedly from a bilaterian body plan than any other group [7,8].

Yet while the five extant echinoderm body plans are clearly differentiated by the Ordovician, tracing these clades back into the Cambrian has proved to be problematic. This is especially true of the crinoids, the most basal extant branch of the echinoderm tree. Undisputed crinoids first appear at or close to the base of the Ordovician [9–11] and possess true arms; that is to say, appendages with a central lumen that are directly connected to the theca and presumably carried coelomic extensions of the body cavity, as in all living crinoids. Some workers have proposed that crinoids are related to Cambrian stalked echinoderms with a different form of feeding appendages (blastozoans [12]) while others have argued for their origin from a group lacking appendages (edrioasteroids [9,10]). For some, then, the origin of feeding appendages in crinoids and blastozoans is a classic example of convergent evolution [13]. Alternatively, free appendages may have arisen just once, and echinoderms, like arthropods, may simply display high levels of phenotypic plasticity in the way their skeletons are constructed. A key question then is whether any blastozoan group ever possessed true arms homologous to those of crinoids [13,14]. Unfortunately, all blastozoans are extinct and so soft tissue reconstruction has to be based on secondary evidence (principally whether the appendage has a large lumen in direct continuity with the main body chamber).

Here, we describe a new family of primitive stalked blastozoan echinoderms from the earliest Middle Cambrian of southwestern Europe that possessed true arms, though ones constructed in a different way from those of crinoids. This group shows a surprising level of phenotypic flexibility in the organization of the supporting skeleton of these arms, and demonstrates that feeding appendages of at least some blastozoans are no different to those of crinoids in their fundamental organization.

## 2. MATERIAL AND METHODS

*Dibrachicystis purujoensis* gen. et sp. nov. and *Vizcainoia moncaiensis* gen. et sp. nov. come from the uppermost part of the Murero Formation at Purujosa, 2 km south of Purujosa village, Moncayo Natural Park, in the northern part of the Iberian Chains, northeast Spain, (see fig. 1 of [15] for details). This primarily siliciclastic succession was deposited under transgressive conditions in an offshore environment during the Caesaraugustan and Lower Languedocian. *Vizcainoia languedocianus* (Ubaghs) comes from deposits of a similar age and environment near Coulouma in the Montagne Noire, southern France [16]. The levels yielding specimens correlate with the Cambrian Series 3, Stage 5 in the Global Stratigraphic System (*ca* 510 Ma).

* Author for correspondence (samuel@unizar.es).

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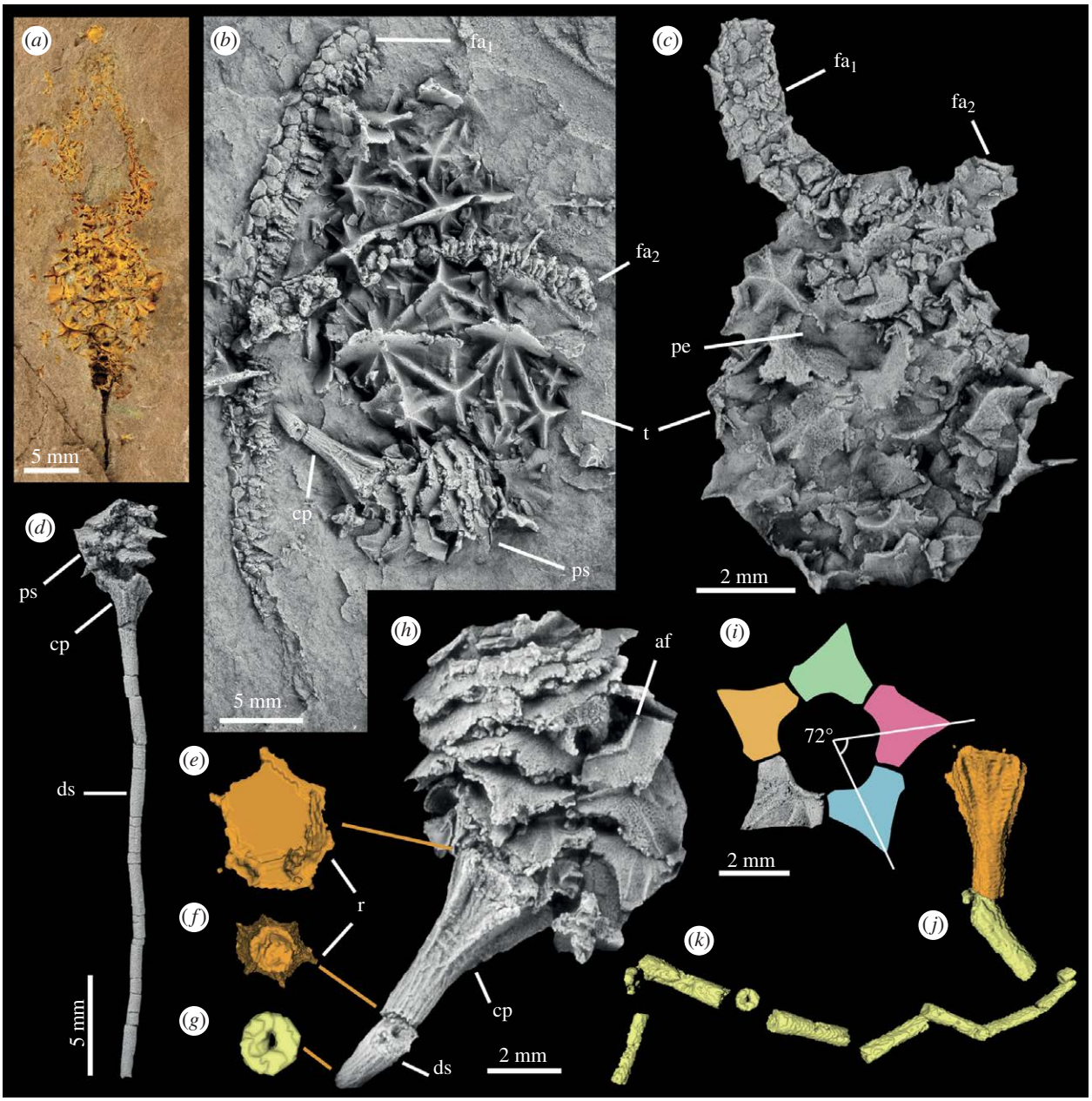


Figure 1. *Dibrachicystis purujoensis* gen. et sp. nov. (*a*) MPZ2011/2, natural mould of complete individual. (*b*) MPZ2009/1236, theca, arms and proximal part of stem. (*c*) MPZ2011/3, theca and basal part of arms. (*d*) MPZ2011/4, tripartite stem. (*e–g*,*j*,*k*) CT model reconstruction of stem based on MPZ2009/1236. (*h*) MPZ0001, proximal part of stem and cone-shaped plate. (*i*) MPZ2011/5, single ossicle of proximal stem and reconstruction. Abbreviations: af, articulation flange; cp, conical plate; ds, distal stem; $fa_1$, $fa_2$, feeding appendages (arm); pe, periproct opening; ps, proximal stem; t, theca. (*b–d*,*h*,*i*) Latex casts.

Two of the best-preserved specimens of *D. purujoensis* were studied using the Metris X-Tek HMX ST computed tomography (CT) system at the Natural History Museum, London. High-resolution slices were obtained and a three-dimensional model of its anatomy built using the software Spiers [17]. The better of these was used to build a three-dimensional model based on 1862 digital slices that were treated independently. Isolated plate boundaries were impossible to differentiate internally owing to the absence of infilling sediment, impeding a full reconstruction of these elements. Plating and stereom details are better observed from latex casts. The most important contribution from the CT scan was accurate reconstruction of the arm structure, a key character in the discussion (see above).

A cladistic analysis was carried out using the software PAUP* [18] to establish this new taxon's phylogenetic position. We included all nine Cambrian stalked echinoderms whose morphologies are well known (electronic supplementary material, table 1), as well as two representative Early Ordovician crinoids (*Aethocrinus* and *Titanocrinus*) and an Ordovician glyptocystitid and pleurocystitid. As root, we used the Lower Cambrian *Kinzercystis*, which is generally considered basal to all stalked echinoderms [19–21]. Twenty-eight skeletal characters were identified as phylogenetically informative and scored. Character descriptions and the resultant data matrix are provided as the electronic supplementary material. A branch-and-bound search was carried out with all characters equally weighted and unordered. Bootstrap values are based on 1000 random addition replicates.

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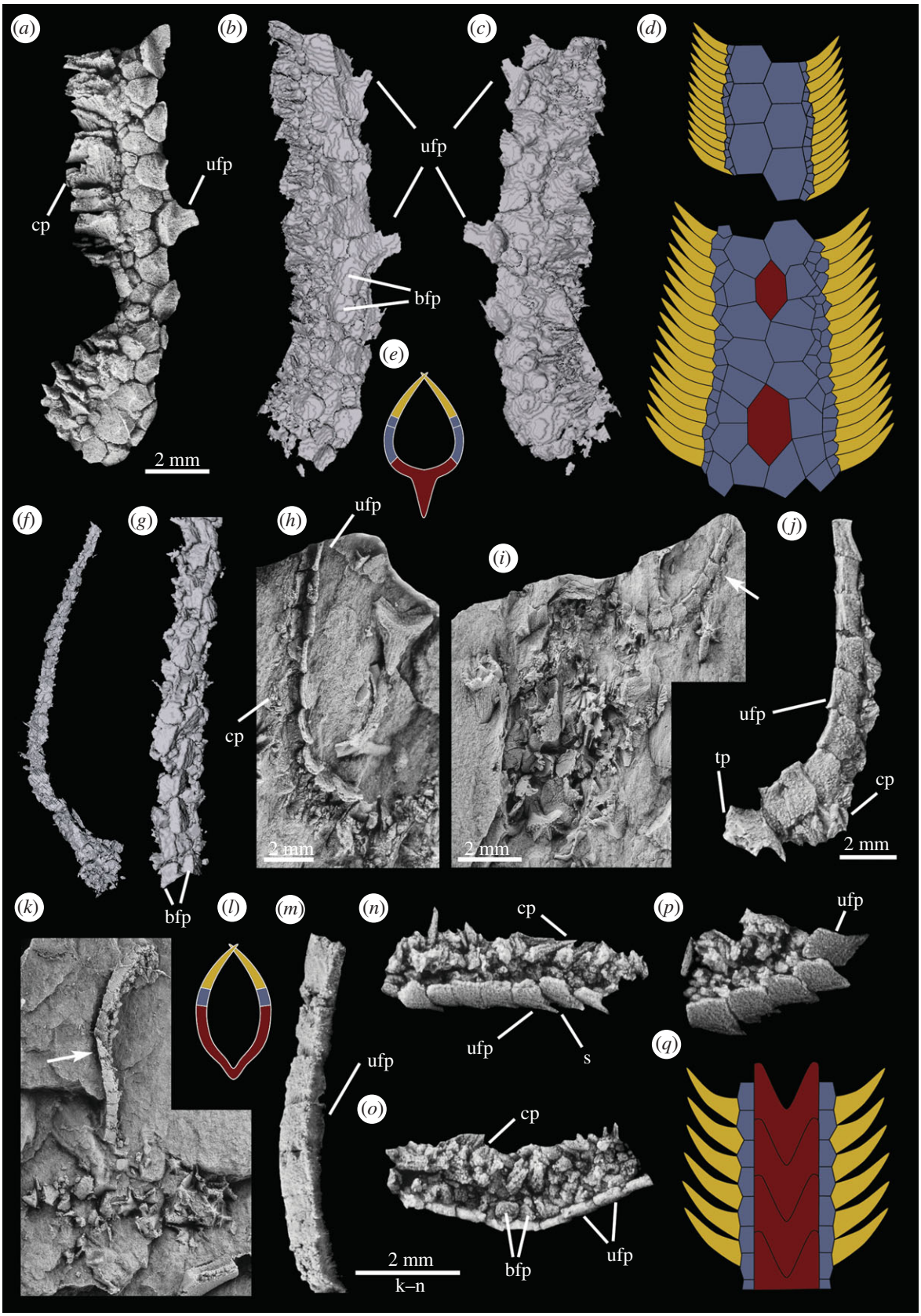


Figure 2. (*a–g*) *Dibrachicystis purujoensis* gen. et sp. nov., MPZ2009/1236. (*a*) Proximal part of one arm in lateral view. (*b*,*c*) CT model reconstruction of base of arm in left and right lateral views. (*d*) Schematic reconstruction of distal (upper) and proximal (lower) arm: cover plates yellow, uniserial flooring plates red and other flooring plates grey. (*e*) Reconstructed cross-section. (*f*,*g*) CT model reconstruction of almost complete arm showing biserial flooring plates distally (*g*). (*h–j*) *Vizcainoia languedocianus* Ubaghs (1987), Muséum National d'Histoire Naturelle, Paris (MNHN A38542). (*h*,*i*) Proximal arm and partial theca in part and counterpart. (*j*) Detail of proximal arm. (*k–q*) *Vizcainoia moncaiensis* sp. nov., MPZ2011/7. (*k*) Arm (arrowed) and partial theca. (*l*) Reconstructed cross-section. (*m*) Arm in aboral view. (*n–p*) Three views of arm in lateral and axial views. (*q*) Schematic reconstruction of arm: cover plates yellow, uniserial flooring plates red and other flooring plates grey. Abbreviations: bfp, biserial flooring plate; cp, cover plate; s, spike; tp, thecal plate; ufp, uniserial flooring plate. (*a*,*h–k*,*m–p*) Latex casts.

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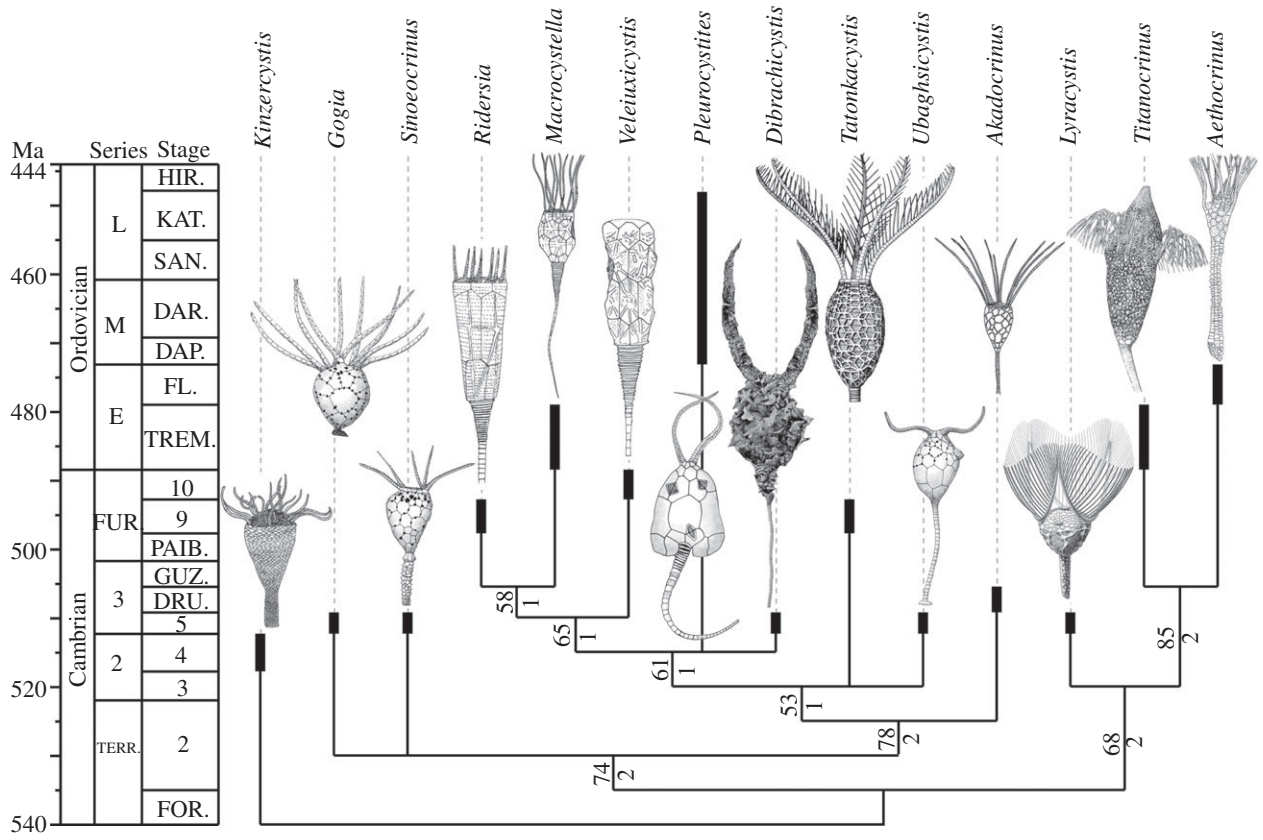


Figure 3. Evolutionary tree of Cambrian stalked echinoderms showing their inferred relationships based on our cladistic analysis. DAP., Dapingian; DAR., Darriwilian; DRU., Drumian; E, Early; FL., Floian; FOR., Fortunian; FUR., Furongian; GUZ., Guzhangian; HIR., Hirnantian; KAT., Katian; L, Late; M, Middle; PAIB., Paibian; SAN., Sandbian; TERR., Terreneuvian; TREM., Tremadocian. Bootstrap support values are to the left of each node and Bremer support values to the right.

## 3. RESULTS

### (a) *Morphology of* Dibrachicystis *gen. nov.*

*Dibrachicystis* has a globular to ovate theca composed of large polygonal plates irregularly arranged and of various sizes (figure 1*a–c*). Plates on their exterior surface have strong, radially arranged ribs matched internally by radial furrows: epispires are wanting. A large glyptocystitid-like periproct opens laterally, framed by distinctive L-shaped plates (figure 1*c*). Two large-plated arms arise from a spout-like oral region, each with a voluminous central cavity that leads directly from the theca (figure 1*a*,*c*). Proximally, arms are constructed of biserially arranged flooring plates that alternate with a uniserial row of large aboral plates bearing blade-like spines, plus additional small intercalated elements (figure 2*a–e*). Plating at the base of the arm grades seamlessly into thecal plating. Distally, the arm is floored by a simple biseries of flooring plates (figure 2*d*,*g*). Overlying these flooring plates comes a multiplated series of small tessellate plates and a biseries of large, flange-like elements (figure 2*a*). In a closely related genus, *Vizcainoia* gen. nov., the arms have an equally large lumen but are floored by a uniserial, slightly imbricate-to-tessellate series of V-shaped plates (figure 2*h–q*). *Dibrachicystis* has a well-developed stalk at the opposite end of the theca to the arms, which has three distinct regions (figure 1*d*). The proximal part of the stalk encloses a large lumen and is constructed of pentameric rings of spiked ossicles (figure 1*i*). These have a clear articulation ring around their inner edge. Distal to this is a circlet of organized plates (see electronic supplementary material, figure S1*e*) mounted on a single large hexameric cone-shaped ossicle that tapers distally (figure 1*e*,*f*). Finally, there is a long distal stalk of cylindrical holomeric columnals without crenulae (figure 1*j*,*k*) but with a small elliptical central lumen (figure 1*g*,*k*).

### (b) *Phylogenetic relationships*

Our analysis of the data matrix given in the electronic supplementary material generated six equally parsimonious trees, whose strict consensus is shown in figure 3. This shows *Dibrachicystis* is not closely related to the early crinoids, but falls in trichotomy with glyptocystitids and pleurocystitids and is more derived than either *Akadocrinus* or the two gogiid genera (*Gogia, Sinoeocrinus*).

## 4. DISCUSSION

The discovery that a group of primitive blastozoan echinoderms have feeding appendages that arise as thecal extensions of the body, demonstrates unambiguously for the first time that arms are not unique to crinoids. Unlike the ‘exothecal ambulacra’ of Sprinkle *et al.* [22], plating of these appendages merges seamlessly into the thecal plating and they bear no brachiolar offshoots. Critically, we have found that, moving from proximal to distal along the length of a single feeding appendage of *Dibrachicystis*, plating changes from that of a polyplated arm with large lumen and uniserial intercalated elements to that of a brachiole with biserial flooring plates and

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proportionally smaller lumen. Polyplated proximal arms are also seen in some at least one protocrinoid (*Apektocrinus* [10]) and a Cambrian crinoid-like blastozoan (*Lyracystis* [23]). This shows that a clear-cut distinction between arms and brachioles may not always be possible to draw, and that in at least one major clade of blastozoans, feeding appendages appear to have originated as direct extensions of the body, and thus incorporated a coelomic component.

Arm-plating structure in dibrachicystids is surprisingly variable, being uniserial in *Vizcainoia* but biserial or triserial in *Dibrachicystis*. A similar variation is found in Middle Cambrian solutes, where *Coleicarpus* has uniserially plated arms but *Castericystis* has biserially plated arms. The variety of different ways feeding appendages are constructed in the Cambrian shows that plating organization was highly flexible and only later came to be stereotypic. While dibrachicystids have arms that arise as direct outgrowths of the body as in crinoids, they are different in construction to those of protocrinids, where a biseries of flooring plates is largely internalized (see [9,10]).

Dibrachicystids bear strongest resemblance to pleurocystitids, a group of Lower Palaeozoic echinoderms with a flattened theca, two arms and a large periproct occupying most of one side. Pleurocystitids first appear in the Middle Ordovician and are thought to be close relatives of the five-armed glyptocystitids [24]. Pleurocystitids and glyptocystitids share a number of derived features, including a distinctive proximal stalk with a large lumen and ring-like elements, a large lateral periproct framed by L-shaped plates, and a standardized cup construction composed of four cycles of plates. However, our analysis finds a surprising amount of homoplasy, implying a high degree of flexibility in the way the skeleton is laid down. Not only is the periproct position rather variable in this group (oral, lateral or in large-framed opening), but neither *Dibrachicystis* nor *Macrocystella* possess pectinirhombs or similar respiratory structures, suggesting these may have evolved in parallel from the strongly pleated plate structure they share. Pleurocystitids, as blastozoans, are generally interpreted as having brachioles, not arms. While their two appendages attach to thick facets, these connect directly to the oral area, as in *Dibrachicystis*, and in structure closely resemble the distal part of the arm of *Dibrachicystis*. It is therefore possible that these appendages are really derived arms.

Finally, while glyptocystitids (*Velieuxicystis*, *Ridersia*) and two-armed 'eocrinoids' (*Ubaghsicystis*) extend into the Late and Mid-Cambrian, respectively, our analysis implies that divergence of rhombiferan lineages was already under way in the Mid-Cambrian.

## 5. SYSTEMATIC PALAEONTOLOGY

Phylum, Echinodermata.

Plesion, Rhombifera.

Family, Dibrachicystidae nov.

*Diagnosis*. Stalked pelmatozoan with theca of many large stellate plates not organized in circlets and large marginal periproct framed by L-shaped plates. Two large arms arise from a spout-like oral area; arms with a large proximal lumen and uniserial elements at least proximally. Stalk tripartite with large proximal pentameric region, holomeric distal region and intermediate cone-shaped element.

*Dibrachicystis* gen. nov.

Type and only known species, *D. purujoensis* sp. nov.

*Locality and horizon*. As for type species.

*Diagnosis*. As for type species.

*Dibrachicystis purujoensis* sp. nov. (figures 1*a–k* and 2*a–g*).

*Derivation of the name*. *Dibrachicystis* refers to the two arms borne by this animal and *purujoensis* to the type locality.

*Types*. Holotype: Zaragoza University Museum MPZ2009/1230. Paratypes: MPZ2011/2–6.

*Locality and horizon*. Purujosa, Section 3, Moncayo Natural Park, northernmost Iberian Chains, northern Spain. *Solenopleuropsis thorali* Zone, Lower Languedocian, early Middle Cambrian.

*Diagnosis*. Arms polyplated proximally with aboral spike-bearing plates uniserially arranged; becoming biserial distally. Cover plates large, flattened and imbricate. Stem tripartite with a pleuromeric fivefold symmetrical proximal part, intermediate cone-shaped plate and distal holomeric part.

*Description*. See the electronic supplementary material.

*Vizcainoia* gen. nov.

*Derivation of the name*. In honour of the amateur palaeontologist Daniel Vizcaïno (Carcassonne, France), who found the first specimen preserving feeding appendages.

*Type species*. '*Eocystites*' *languedocianus* Ubaghs (1987).

*Diagnosis*. Theca as in *Dibrachicystis*. Proximal part of arm constructed primarily of uniserial flooring elements with just occasional very reduced additional intercalated plates.

*Vizcainoia languedocianus* Ubaghs (1987) (figure 2*h–j*).

v 1987. *Eocystites languedocianus* [16], p. 18, pl. 3, figs 1–3.

*Types*. Holotype: Muséum National d'Histoire Naturelle, Paris F.A38500.

*Diagnosis*. Uniserial elements of arm with an aboral keel but lacking distal spiny projections. Thecal plates with strong keel-like expansion of primary ribs.

*Locality and horizon*. Montagne Noire (France). *Solenopleuropsis* (*Solenopleuropsis*) Zone, Lower Languedocian, early Middle Cambrian [16].

*Description*. See the electronic supplementary material.

*Vizcainoia moncaiensis* sp. nov. (figure 2*k–q*).

*Derivation of the name*. Refers to the Moncayo Mountains, Spain, from where the material is derived.

*Types*. Holotype: MPZ2011/7.

*Diagnosis*. Uniserial elements of arm with a spike-like aboral projection.

*Locality and horizon*. Purujosa, Section 6, Moncayo Natural Park, northernmost Iberian Chains, northern Spain. *Pardailhania multispinosa* Zone, middle Caesaraugustan, early Middle Cambrian.

*Description*. See the electronic supplementary material.

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