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THE ONTOGENY OF CINCTANS (STEM-GROUP ECHINODERMATA) AS REVEALED BY A NEW GENUS, *GRACIACYSTIS*, FROM THE MIDDLE CAMBRIAN OF SPAIN

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Abstract: A new cinctan echinoderm, *Graciacystis ambigua* gen. et sp. nov. from Cambrian Series 3 rocks of Spain, is described based on more than 100 articulated specimens that range from 6 to 14.5 mm in thecal length. This material shows that *Graciacystis ambigua*, while plastic in thecal shape, is highly conservative in its thecal construction, with a fixed number of marginal plates and very limited addition of plates in the stele and ventral membrane through ontogeny. Ventral swellings on marginal elements are absent from the smallest specimens and become gradually more marked during growth. A cladistic analysis shows *Graciacystis* to be a basal cinctan, more derived than *Sotocinctus* and the Trochocystitidae and as sister group to a large clade formed by Sucocystidae + Gyrocystidae. The determinate growth pattern seen in *Graciacystis* seems to be the general pattern for all cinctans.

Key words: Echinoderms, stem-group, ontogeny, phylogeny, cinctans, Cambrian.

CINCTANS are nonradiate echinoderms known solely from the middle Cambrian of Gondwana (including Avalonia) and Siberia, with currently 15 genera and 25 species formally described (Smith and Zamora 2009). These animals are constructed with a flattened, asymmetrical body (theca) and a stout posterior appendage (stele). The theca consists of a rigid marginal ring of stout plates (the cinctus), which frames dorsal and ventral membranes of thin tessellated plates (the supracentral and infracentral integuments, respectively). A circular mouth associated with one or an unequal pair of marginal feeding groove(s) opens through the right anterior margin of the cinctus; a larger opening (the porta) covered by a moveable plate (the operculum) pierces the anterior of the marginal frame more centrally. The stele is short and rigid, arising as a direct extension of the cinctus (Jefferies 1990).

Cinctans are the most diverse echinoderm clade known from the middle Cambrian soft ground communities of western Gondwana (Zamora and Álvaro 2010). However, a notable gap occurs in their fossil record during the middle Caesaraugustan Mediterranean stage (Zamora and Álvaro 2010) – a critical interval in cinctan evolution; several taxa last appear in the lower Caesaraugustan (e.g. *Asturicystis* and *Sotocinctus*), while others first occur in the uppermost middle Caesaraugustan (e.g. *Gyrocystis*).

In this study, we describe a new cinctan from the northern part of the Iberian Chains, Spain that is middle Caesaraugustan in age, thereby filling an important gap in the cinctan fossil record. Furthermore, this genus is erected based on a large collection of both juveniles and adults, thereby allowing the ontogeny and intraspecific variability of cinctans to be elucidated in detail for the first time.

GEOLOGICAL SETTING AND STRATIGRAPHY

The specimens described in this study were collected in the northern part of the Iberian Chains (northeast Spain), from a locality near Purujosa village in the Moncayo Natural Park, Zaragoza province (Fig. 1). Two kilometres to the south of Purujosa, Cambrian outcrops are common; they are separated from Mesozoic rocks by the Jarque fault (Samaniego *et al.* 1972). Here, a succession of rocks crops out spanning some 10 million years from the

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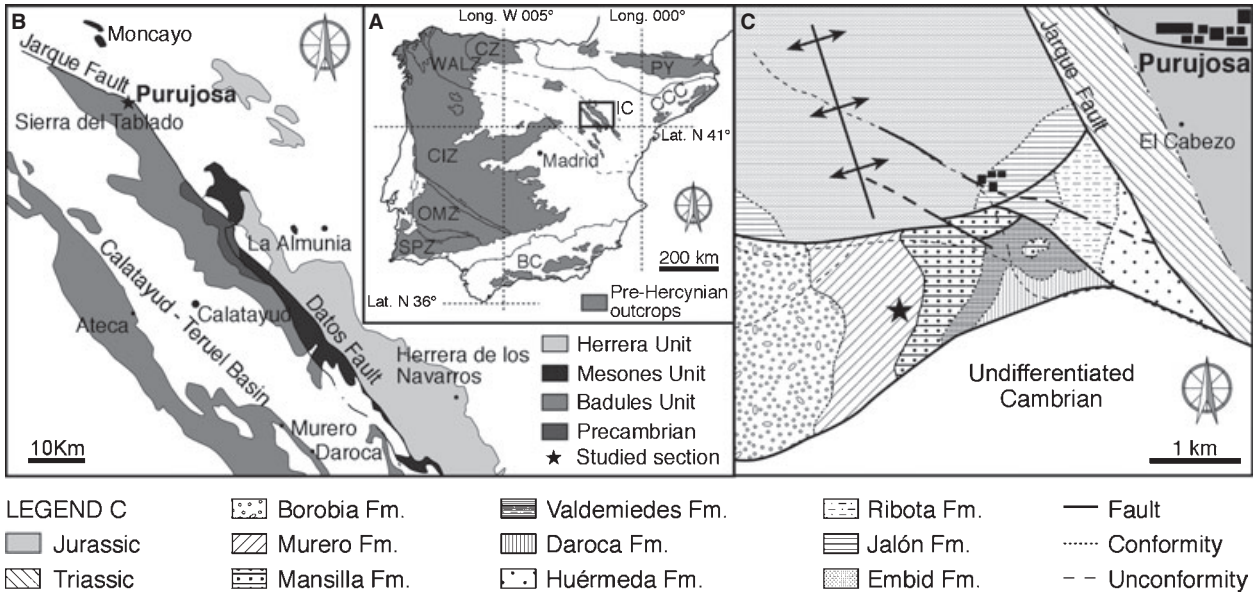

FIG. 1. Locality maps showing where the specimens of *Graciacystis* were collected. A, general map of Spain showing the position of the Iberian Chains. B, detail of the northernmost part of the Iberian Chains. C, geological map of the studied area. The star marks the fossil locality.

uppermost lower Cambrian to the middle Cambrian and including the Daroca, Valdemiedes, Mansilla, Murero and Borobia formations (Fig. 1C). Echinoderms are common in the last three formations including cinctans, ctenocystoids, stylophorans, edrioasteroids and various blastozoan grade echinoderms (Rahman and Zamora 2009; Zamora 2010, 2011; Zamora and Álvaro 2010; Zamora and Smith 2010, 2012).

Graciacystis ambigua gen. et sp. nov. was collected between 5 and 25 m above the base of the Murero Formation, in the Pur6 section (Fig. 2). Here, the Murero Formation consists of 75–100 m of shales with interbedded carbonate nodules. Cinctans occur in various stratigraphic levels from the top of level three up to level nine (Fig. 2), but are especially common in the latter, where they are found in green shales together with a diverse associated fauna including the echinoderm *Vizcainoia moncaiensis* and the trilobites *Badulesia tenera*, *Pardailhania hispida*, *Pardailhania multispinosa*, *Eccaparadoxides sequeirosi*, *Parabailella languedocensis*, *Ctenocephalus antiquus* and *Peronopsis*? sp. The associated trilobite assemblages occurring in these levels indicate a stratigraphic range of *Graciacystis ambigua* gen. et sp. nov. from the *Badulesia granieri–Pairdailhania multispinosa* zones, which is indicative of a lower–middle Caesaraugustan age. In global terms, the correlation of these levels is problematic; based on chemostratigraphic data this corresponds to Stage 5 of Cambrian Series 3 (Álvaro *et al.* 2008) but base on the trilobite species and their correlation this corresponds with the base of the Drumian (Gozalo *et al.* 2011).

MATERIAL AND METHODS

More than one hundred specimens of the new cinctan were collected during a large-scale excavation at Purujosa 6 (or Pur6) in October 2009; many of these specimens are fully articulated, suggesting rapid burial, and all are preserved as moulds coated with iron oxide. Prior to study, specimens were submerged in an oxalic acid solution for approximately 1 day. This removed the iron oxide residues, allowing the observation of fine details including stereom microstructure. Specimens were consolidated using a paraloid solution (5–7 per cent) and latex casts of the fossils were produced. Photographs of latex casts were taken after they had been whitened with ammonium chloride sublimate.

Only undistorted specimens were selected for measurement. Because the studied area has not been subjected to strong tectonic deformation, the specimens are preserved with close to the original shape, and the measurements are thus representative of life sizes. In around 20 per cent of the specimens, one or two plates are slightly displaced from their original positions. In these cases, the positions of plates were corrected following the original articulations and measurements were taken after correction. The Pearson correlation coefficient (r) was used to measure the association between selected measures of thecal size.

Repository. All of the specimens are housed in the Área y Museo de Paleontología, Universidad de Zaragoza (Spain), under repository numbers MPZ 2012/177 to MPZ 2012/287.

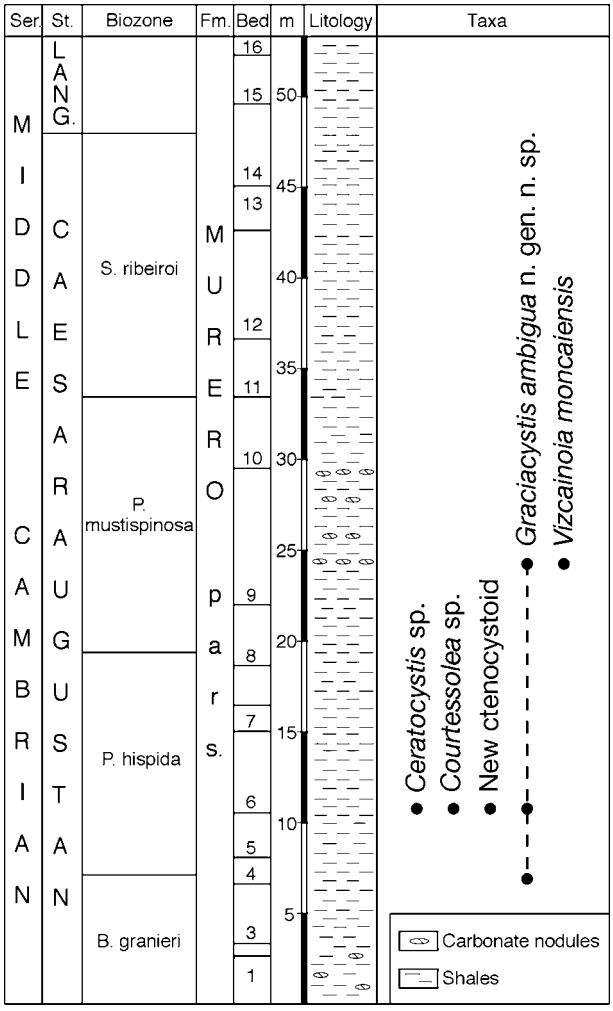

FIG. 2. Stratigraphic section (Pur6) showing the distribution of the echinoderm fossils collected.

SYSTEMATIC PALAEONTOLOGY

Phylum ECHINODERMATA Bruguière, 1791 (*ex* Klein, 1734)
Class CINCTA Jaekel, 1918

Genus GRACIACYSTIS gen. nov.

Type species. Graciacystis ambigua sp. nov.

Derivation of name. The genus is named after the amateur palaeontologist Fernando Gracia, who first found the level where the specimens occur, in recognition of his continuous support collecting Cambrian echinoderms.

Diagnosis. As for the type species.

Discussion. Graciacystis is distinguished from *Gyrocystis*, *Progyrocystis* and some species of *Sucocystis* (*S. bretoni*, *S. theronensis*) by possessing left and right food grooves rather than a single left food groove. Furthermore, the left food groove is longer than in the Gyrocystidae, extending over one more marginal plate in *Graciacystis*. *Graciacystis* also has a larger number of plates in the lintel (6–8 as opposed to 3–4 in *Gyrocystis* and *Progyrocystis*). In *Sucocystis* species with left and right food grooves, such as *S. acrofera*, the right one is longer than in *Graciacystis*. *Undatacinctus* and *Lignanicystis* both share a similar arrangement of food grooves with *Graciacystis*. *Graciacystis* is distinguished from *Undatacinctus* by the lack of dorsal protuberances in its cinctus. *Lignanicystis* has more numerous ventral swellings and also a more asymmetric thecal shape than *Graciacystis*. *Asturicystis*, *Sotocinctus*, *Trochocystites* and *Trochocystoides* all have much longer food grooves than *Graciacystis*. Only *Asturicystis* and *Sotocinctus* have the same plesiomorphic undifferentiated arrangement of plates in the lintel as in *Graciacystis*.

Graciacystis ambigua sp. nov.
Figures 3–6

Derivation of name. From the Latin *ambigua* in reference to the very variable shape of the theca in this species.

Holotype. MPZ 2012/177 (Fig. 4C–D), a complete, articulated specimen preserved as a mould in a siltstone.

Paratypes. Thirty-one specimens (MPZ2012–178-208) preserved in siltstones as moulds, many of them as part and counterpart and fully articulated in the most cases.

Diagnosis. A cinctan with a variable thecal shape (subtriangular, oval or circular); cinctus composed of 10 or (rarely) 11 marginal plates (M5r–M4l or M5r–M5l). Two food grooves, one extending to M1l and the other up to M2r. Dorsal integument with a continuous row of epispires in the right side. Ventral surface flat in juveniles but with a single anterior swelling developed in adults. Adopercular processes weakly developed and lintel composed of 6–8 plates.

Type locality. Pur6 section, between 5 and 25 m above the base of the Murero Formation, 2 km south of Purujosa village, in the northern part of the Iberian Chains, Spain.

Type stratum. Murero Formation, middle Caesaraugustan, middle Cambrian (Cambrian Series 3, Stage ?5).

Description. In this description, nomenclature and orientation follow Friedrich (1993); this is the optimal scheme for recognizing homologies among cinctan taxa (Smith and Zamora 2009). Briefly, the marginal plate that coincides with the axial plane is named M0, and the remainder of the marginal plates are numbered as M1r–M5r or M1l–M5l (Fig. 3), depending on whether their position is right or left of M0 (in plan view).

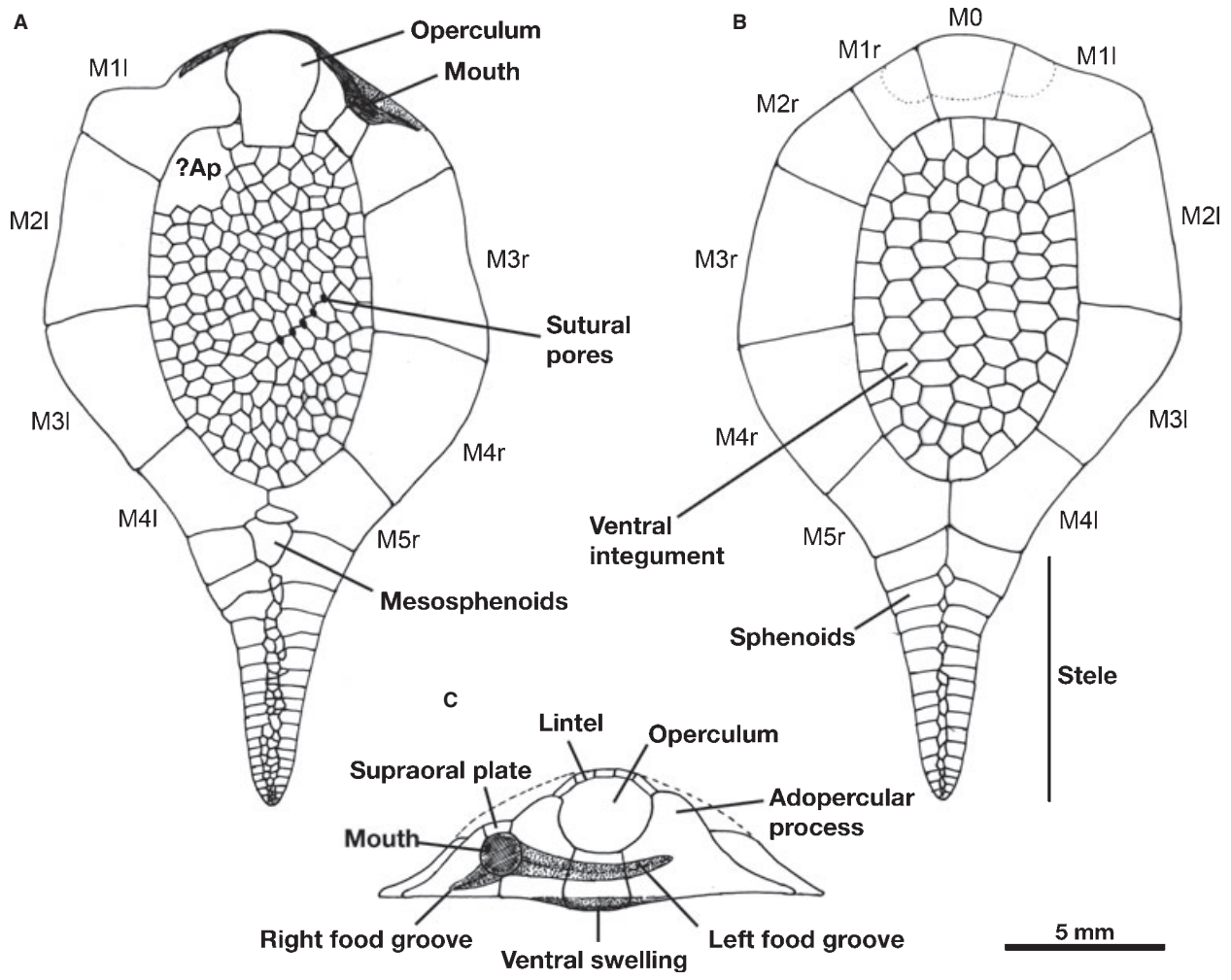

FIG. 3. *Graciacystis ambigua* gen. et sp. nov. from the middle Cambrian of Purujosa (Iberian Chains, Spain). Reconstruction in dorsal, ventral and frontal views showing the main anatomical elements. Abbreviation: Ap, anal pyramid.

The theca consists of 10 or rarely 11 marginal plates (M5r–M4l or M5r–M5l) and several hundred integument plates. It ranges in size from approximately 6–14.5 mm in length and 6–16.5 mm in width; the thecal outline is oval to subtriangular (in smaller specimens) or oval to circular (in larger specimens; Fig. 5). The stele measures approximately 7–14 mm in length.

Orifices. Three openings occur in the theca of *Graciacystis* (Fig. 3).

1. A small circular aperture passes through the anterior right side of the cinctus between marginal plates M1r and M2r and is covered dorsally by the supraoral plate (Fig. 4F–G). The opening is slightly flattened dorsoventrally and is wider than tall in external view (approximately one mm wide in the holotype). On the interior, M1r and M2r form a broad, expanded platform ventral to the opening. Externally, two marginal grooves lead from the left and the right into this aperture.
2. The largest aperture (the porta) lies at the anterior of the theca, passing through the marginal frame coincident with the axial plane. This opening is covered by a large, spoon-shaped plate known as the operculum and is bounded ventrally and laterally by marginal plates M0, M1l and M1r. The upper margin of the opening is bordered by six to eight plates of the supracentral integument (the lintel; Fig. 4A, E). The operculum is approximately three mm in length in the axial direction and two mm in width and completely filled the porta during life (Fig. 4F). It is smooth on its inner concave face, but ornamented on its external, convex face.
3. A uniserial row of small circular openings occurs towards the right of the supracentral integument. In the best-preserved specimen, at least five openings are present (Fig. 4C–D). Each opening is approximately 200 μm in diameter and lies along the sutures between multiple (four or five) supracentral plates. These are the dorsal sutural pores.

Cinctus. The cinctus is composed of 10 or rarely 11 marginal plates, which vary in size and shape around the ring (Fig. 3). All are approximately triangular in cross-section, with short, thick, concave internal faces and wide, wedge-shaped outer faces.

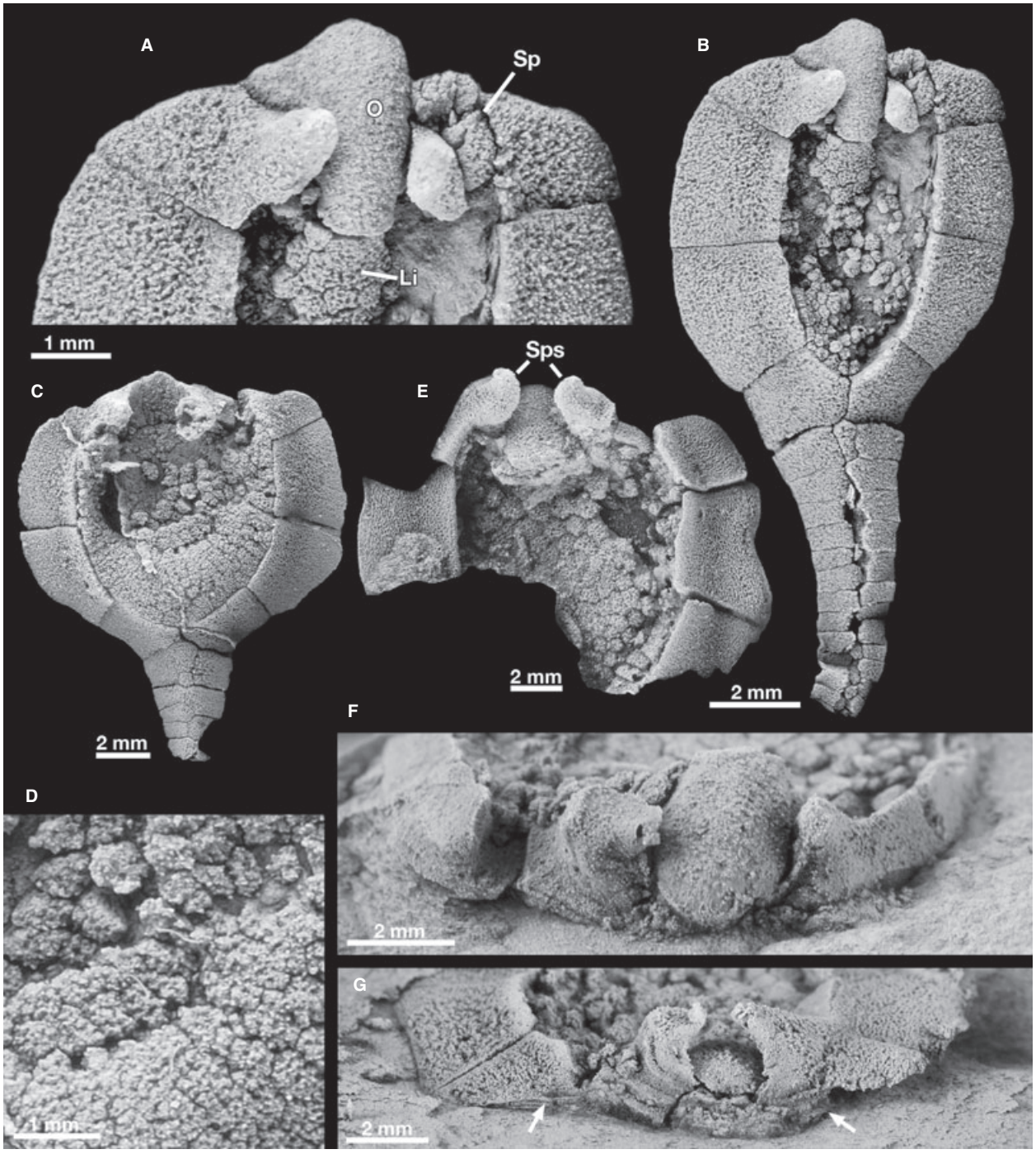

FIG. 4. *Graciacystis ambigua* gen. et sp. nov. A, paratype MPZ2012/186a; detail of the porta-operculum complex in a relatively small specimen showing the operculum, adopercular processes and lintel composed of multiple supracental plates that are not distinct from other supracentral plates. B, general view of the same specimen. C, holotype MPZ 2012/177; medium-sized specimen (10 mm in thecal length) with a well-preserved supracentral integument. D, detail of the supracentral integument in the same specimen showing epispires arranged in an arc. E, paratype MPZ2012/204; anterior part of a large specimen showing the porta-operculum complex. F, paratype MPZ2012/205; frontal view showing the operculum in place. G, paratype MPZ2012/194; frontal view showing the position of food grooves. Arrows indicate the end of marginal grooves. Abbreviations: O, operculum; Sp, supraoral plate; Li, lintel; Sps, adopercular processes. All specimens are latex casts whitened with NH_4Cl sublimate.

M0 is a trapezoidal plate located at the anterior of the cinctus that forms the floor to the porta. It is slightly swollen on its ventral surface, wider at its anterior than posterior in plan view and bears the single marginal groove on its outer face. There is no broad anterior shelf to this plate; the marginal groove runs beneath the ambitus and faces forwards.

M1r and M1l form the lateral frame to the porta, each giving rise to a small dorsal adopercular process (Figs 4A and 5). Both plates are rectangular in ventral view and articulate loosely with the supracentral and infracentral integuments. M1r also articulates with the supraoral plate, M0 and M2r; M1l articulates with M0 and M2l. The suropercular facets mark the articulation points with the plates of the lintel. The adopercular processes are inclined slightly towards the anterior. M1r and M1l carry portions of the marginal groove on their outer surfaces. M2r is hatchet-shaped. The distal part of this plate is expanded outwards as a wide platform, which narrows as it approaches the right circular aperture. M3r is very similar to the other midcinctus plates, having a flat ventral surface with a rectangular outline and an outer flange on its dorsal surface. M4r is slightly longer than M3r. The anterior part of M4r continues the broad outer platform developed on M3r. M5r closes the cinctus at the posterior of the theca and articulates with M4r and M4l. Its posterior margin articulates with the stele.

The left marginal plates of the cinctus (M2l, M3l) are similar to those of other cinctan species; all have a wide margin that becomes slightly narrower as it approaches to the plates near the stele. A single swelling occurs at the anterior of the ventral surface of the cinctus; this occupies the entirety of the ventral surface of M0, extending laterally to M1r and M1l (Fig. 6A–B). All the marginal plates have a similar stereom ornamentation; the outer surfaces (and the exterior of the operculum) show a dense labyrinthic ornamentation, while the ventral surfaces are smooth and unornamented.

Integuments. The supracentral (dorsal) and infracentral (ventral) integuments are composed of a large number of small polygonal plates. The plates forming the infracentral integument are slightly fewer in number and larger than those of the supracentral integument, but the size distribution of plates is more or less uniform in each integument (Fig. 6).

The plates making up the supracentral integument are ornamented externally, but their interior faces are smooth (Fig. 4A, D). The infracentral integument is composed of polygonal tessellate plates. Sutures of supracentral plates bear an invagination for the attachment of ligaments, while infracentral plates show flatter sutures (Fig. 6A, E).

Marginal groove. Marginal grooves (Fig. 3C) run left and right from the mouth around the outer face of the marginal ring to M1l and M2r, respectively (Fig. 4F–G). At the anterior of the theca, the left groove lies below the ambitus, and thus faces frontally. A weakly developed rim borders the marginal groove at the articulation of the labrum plates. The right marginal groove is very short, extending only up to M2r. Some specimens preserve part of the labrum, which is composed of a sheet of small platelets, but is not well enough preserved in any specimen to be described in detail.

Stele. The stele (Fig. 3) originates as a direct continuation of the marginal frame (Figs 5–6). It is approximately as long as the theca. It is constructed from a marginal series of wedge-shaped sphenoid plates, with smaller polygonal mesosphenoidal plates along the dorsal and ventral midlines. A small cavity, bounded by sphenoid plates laterally and mesosphenoid plates dorsally and ventrally, runs the length of the stele. Mesosphenoid plates along the dorsal part of the stele are uniserially arranged proximally, but arranged into an alternating biseries in the distal two-thirds of the stele. In the ventral part of the stele, mesosphenoids are very small and appear as a single series through the entire stele. In cross-section, the stele is triangular.

PHYLOGENETIC POSITION OF *GRACIACYSTIS*

Phylogenetic analysis

The phylogenetic position of *Graciacystis* within the Cincta was assessed by adding it to the character data matrix compiled for cinctans by Smith and Zamora (2009). *Graciacystis* was scored for each of the 57 characters used in that analysis (Table 1 lists these character states) and added to the original 19 cinctan taxa to give a new data matrix of 20 taxa and 57 characters. We used *Asturicystis* as outgroup for rooting purposes, as this was the genus previously identified as the most basal cinctan in the analysis of Smith and Zamora (2009). The new data matrix was subjected to a cladistic analysis using the computer program PAUP* (Swofford 2002). All characters were treated as of equal weight and 13 characters were treated as ordered, as in the original analysis of Smith and Zamora (2009). A branch and bound search was carried out, which is guaranteed to find all the most parsimonious trees. Node support was assessed by running 1000 bootstrap replicates and a Bremer Decay analysis.

Results

Phylogenetic analysis of our new cinctan data matrix found six equally parsimonious cladograms of 145 steps (Consistency Index = 0.53; Retention Index = 0.66; Fig. 7). The strict consensus of these places *Graciacystis* near the base of the Cincta, more derived than *Sotocinctus* and the Trochocystitidae and as sister group to a large clade formed by Sucocystidae + Gyrocystidae. Bootstrap support across the tree is weak but the nodes on either side of *Graciacystis* have a Bremer Support value of 2. Characters supporting the sister group relationships of *Graciacystis* and the Sucocystidae + Gyrocystidae clade mostly relate to the more restricted extent of the marginal groove (characters 46, 47, 51 and 52). Characters that dis-

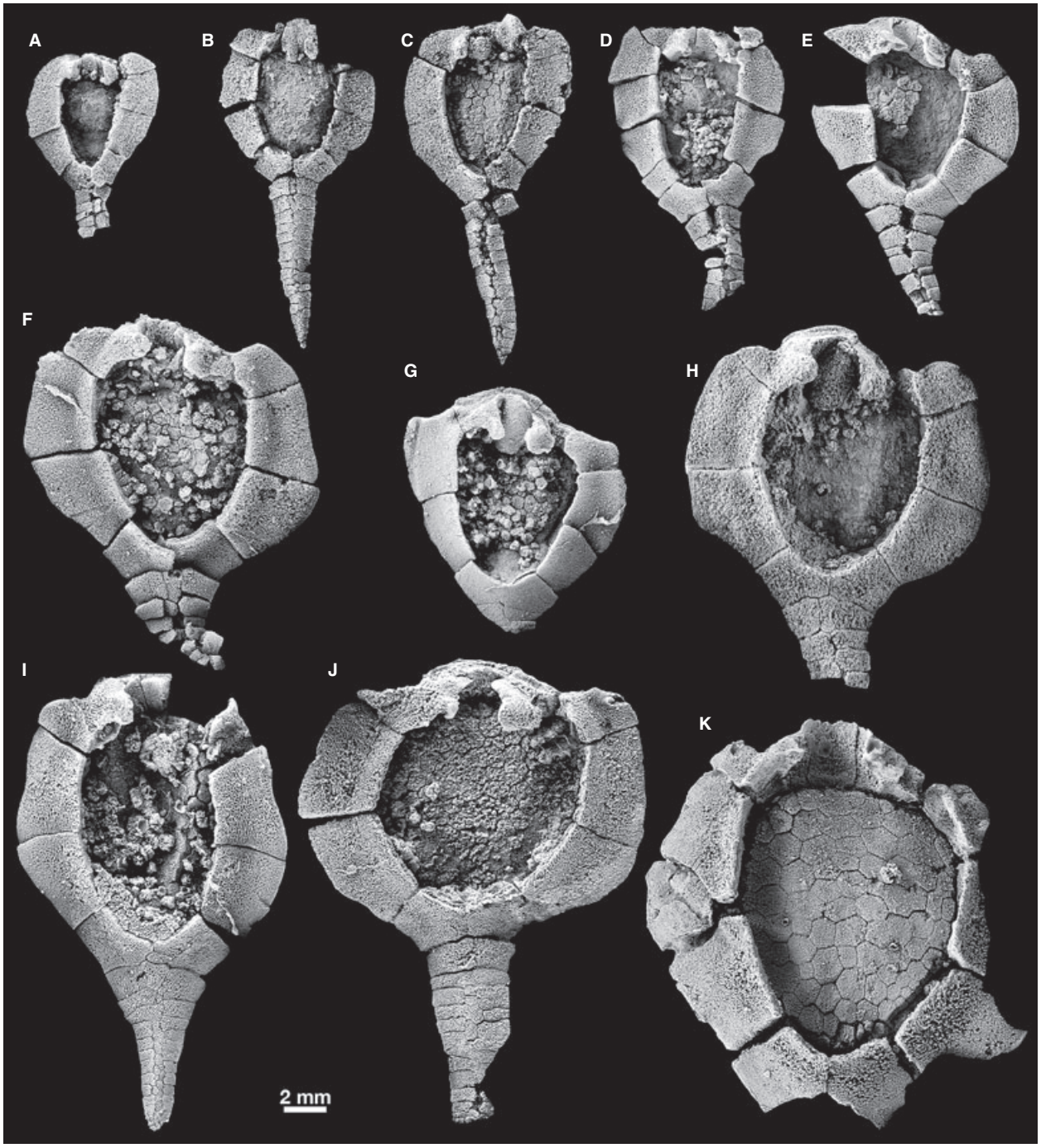

FIG. 5. *Graciacystis ambigua* gen. et sp. nov. Comparative ontogeny of the dorsal surface based on specimens ranging from 6 to 14.5 mm in thecal length. A, paratype MPZ2012/182; smallest specimen with a complete theca bearing 10 marginal plates, a suboval shape and very small adopercular processes, B–C, paratypes MPZ2012/187a, 188; relatively small specimens with very long steles. D, paratype MPZ2012/206; small specimen with an extra marginal plate in the left side of the cinctus. E, paratype MPZ2012/207; medium-sized specimen. F, paratype MPZ2012/184; complete adult specimen with a subcircular theca. G, paratype MPZ2012/181; medium-sized specimen preserving the operculum. H, paratype MPZ2012/196; complete adult specimen preserving part of the stem. I, paratype MPZ2012/183a; complete adult specimen with a more oval thecal shape, retained as a juvenile character. J–K, paratypes MPZ2012/185, 208, largest specimens. All specimens are latex casts whitened with NH_4Cl sublimate.

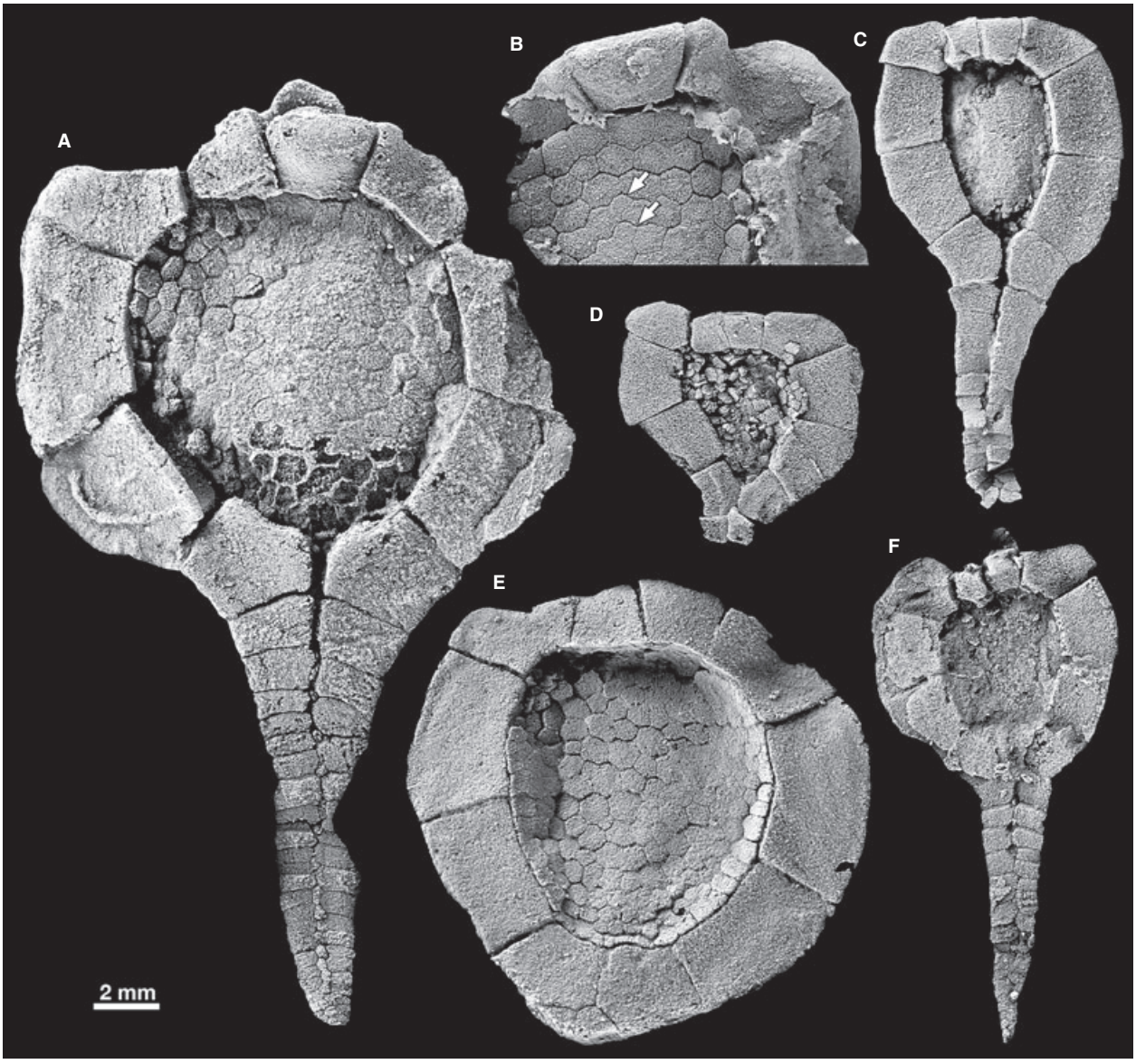

FIG. 6. *Graciacystis ambigua* gen. et sp. nov. Comparative ontogeny of the ventral surface based on specimens ranging from 6 to 14.5 mm in thecal length. A, paratype MPZ2012/192b; very large specimen preserving the theca and complete stele; note the presence of a large ventral swelling in the anterior part and mesosphenoids throughout the stele. B, paratype MPZ2012/203; anterior part of a relatively large specimen showing the anterior swelling; arrows indicate points of new infracentral plates added. C–D, F; paratypes MPZ2012/186b, 200, 187b; small specimens without ventral swellings; note also how they have proportionately less infracentral integument surface compared with larger specimens. E, paratype MPZ2012/195b; medium-sized specimen with a moderately developed swelling. All specimens are latex casts whitened with NH_4Cl sublimate.

TABLE 1. List of 57 character states codified for *Graciacystis ambigua*.

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Character descriptions are given in Smith and Zamora (2009).

tinguish *Graciacystis* from the Sucocystidae + Gyrocystidae clade include its more rudimentary suropercular facet and the more numerous plates forming the lintel. *Graciacystis* also has a right marginal groove that is absent in all Gyrocystidae and some Sucocystidae. However, all of these characters show some degree of homoplasy.

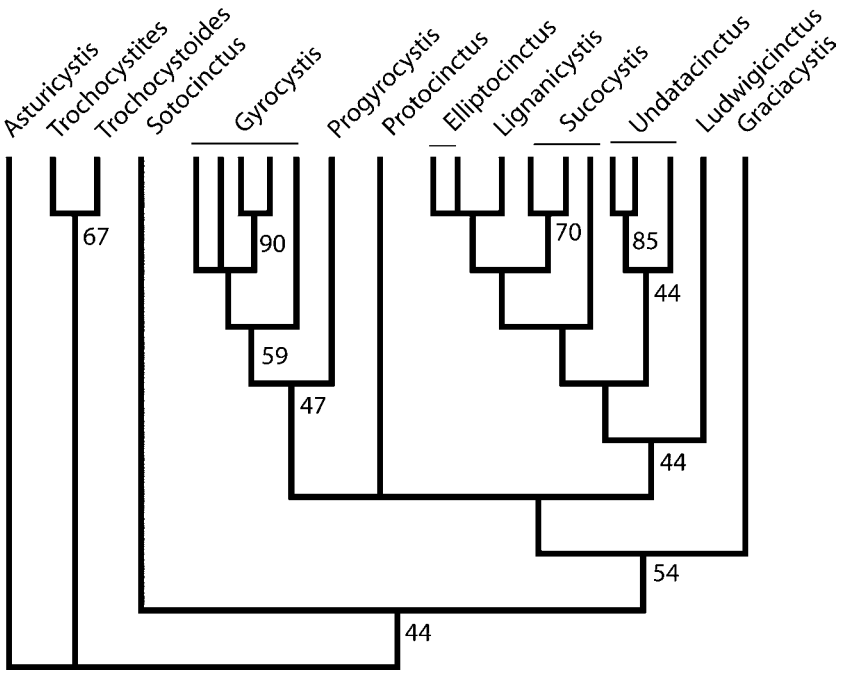

FIG. 7. Strict consensus of the six equally parsimonious cladograms (tree length 145 steps) found in our parsimony analysis. Bootstrap values are provided for all nodes supported at more than 40 per cent and which are still present in trees one-step longer than the most parsimonious solution.

TABLE 2. Measures from the dorsal surface.

Specimen	Length (mm)	Width (mm)	Length/Width
MPZ2012-180	12	12.7	0.945
MPZ2012-181	10	10	1
MPZ2012-182	6.4	5.8	1.103
MPZ2012-183a	13.5	13	1.038
MPZ2012-184	11.9	14	0.85
MPZ2012-185	13	16.5	0.788
MPZ2012-177	10	11.8	0.847
MPZ2012-186a	8	7.3	1.096
MPZ 2012-192a	14.5	15.5	0.935
MPZ2012-193a	12.5	14.5	0.862
MPZ2012-194	12	14	0.857
MPZ2012-195a	13	14.3	0.909
MPZ2012-196	12.8	14.3	0.895
MPZ2012-197a	10	9.7	1.030
MPZ2012-198	13	13.7	0.949
MPZ2012-187a	7	7.2	0.972
MPZ2012-188	7.5	7.5	1
MPZ2012-189	9.5	8	1.187
MPZ2012-190	10	11.6	0.862
MPZ2012-191a	9	10.1	0.891
MPZ2012-178a	11	10.4	1.058
MPZ2012-179	14	15	0.933

ONTOGENY OF *GRACIACYSTIS*

The ontogeny of cinctans has never previously been described in detail. Based on the relatively abundant material of *Graciacystis*, which ranges from 6.4 to 14.5 mm in thecal length (complete list of measurements in Tables 2 and 3), the later, postmetamorphic ontogenetic development of a cinctan genus can now be elucidated for the first time.

The thecal shape is very variable, with the central body cavity ranging from elongate and narrow (Fig. 6C) to broad and shield-shaped (Fig. 6A). The shape is predominantly elongate in juveniles and shield-shaped in adults, and there is a weak negative correlation between thecal length and the thecal length to width ratio ($r = -0.461$, $p = 0.031$; Fig. 8C). Thus, juveniles tend to be longer than they are wide, with width increasing relative to length during ontogeny.

While the shape of the theca is rather plastic, the construction of the theca is highly conserved through later ontogeny. The number of plates in the cinctus is very consistent; all known specimens have 10 marginal plates with the exception of one which displays an extra plate in the left side (Fig. 5D). This suggests that plate number was established at a very early stage in development and did not vary during growth.

The length and number of plates forming the stele is also very similar throughout growth. Over a twofold increase in the size of the theca, the relative length of the stele changes little. One small specimen (7 mm in length) preserving a complete stele shows 18 rows of sphenoids (Fig. 6F). Larger specimens that are approximately double in size (14.4 mm in length) possess just 22 rows of sphenoids (Fig. 6A), indicating that cinctans added only a few sphenoids as they grew. The very conservative way in which the stele is built supports previous ideas that the

TABLE 3. Measures from the ventral surface.

Specimen	Total width	Width marginal plates	Number of infracentral plate rows	Total to marginals width ratio	Integument width
MPZ2012-178b	10.6	4.6	9	2.304	6
MPZ2012-199	10.6	4.5	8 or 9	2.355	6.1
MPZ2012-183b	12.2	5	9 or 10	2.440	7.2
MPZ2012-186b	7.5	4	9	1.875	3.5
MPZ2012-192b	16.5	6.5	11	2.538	10
MPZ2012-195b	13.8	5.8	12	2.379	8
MPZ2012-191b	10	4.6	10	2.174	5.4
MPZ2012-200	7.3	3.8	?	1.921	3.5
MPZ2012-193b	14	4.2	12	3.333	9.8
MPZ2012-187b	7.2	3.4	?	2.118	3.8
MPZ2012-201	8.7	4.4	10	1.977	4.3
MPZ2012-202	12.7	5.6	?	2.268	7.1
MPZ2012-203	?	?	9 or 10	–	–

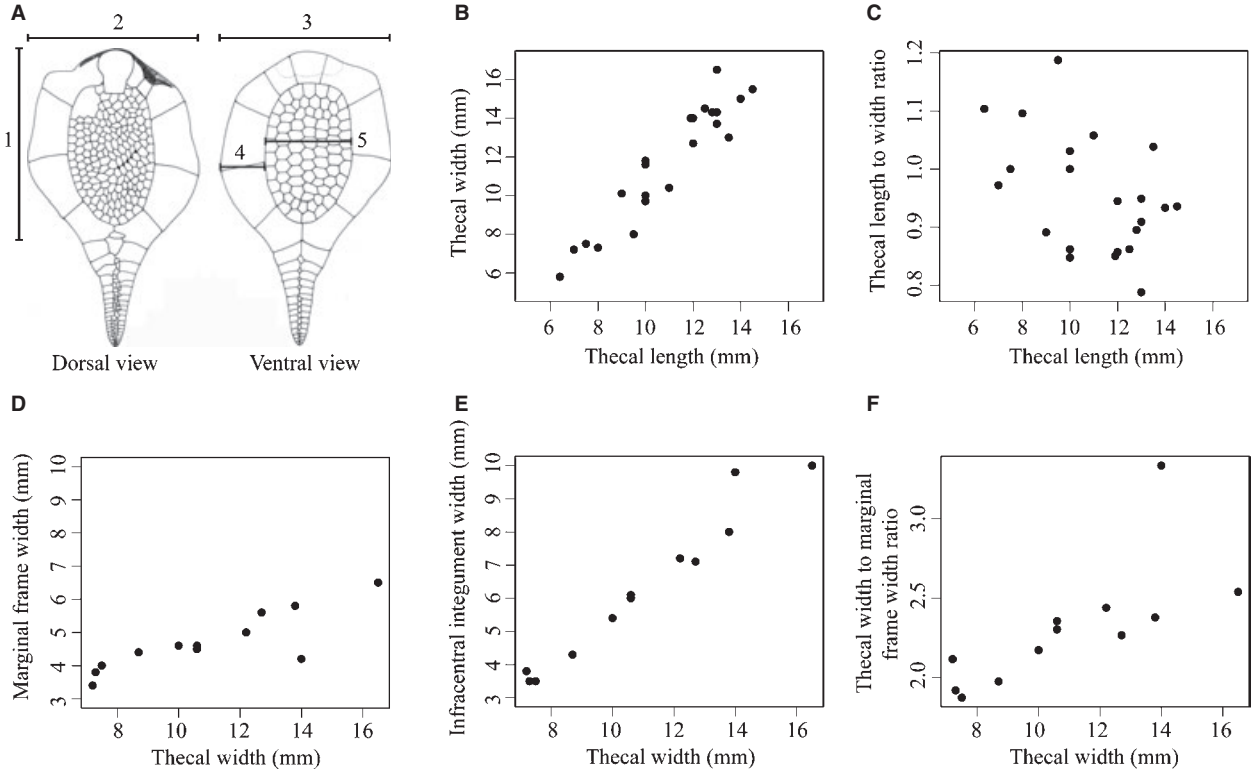

FIG. 8. Body size measures of *Graciacystis ambigua* gen. et sp. nov. A, reconstruction showing where measurements were taken: 1, dorsal thecal length; 2, dorsal thecal width; 3, ventral thecal width; 4, marginal frame width; 5, infracentral integument width. B, relationship between thecal length and thecal width based on measurements of the dorsal surface. C, relationship between thecal length and the thecal length to width ratio based on measurements of the dorsal surface. D, relationship between thecal width and marginal frame width based on measurements of the ventral surface. E, relationship between thecal width and infracentral integument width based on measurements of the ventral surface. F, relationship between thecal width and the thecal width to marginal frame width ratio based on measurements of the ventral surface.

cinctus and stele were part of the same tissue earlier in development (Jefferies 1990) and subsequently followed similar growth pathways. Plates were likely added to the stele through intercalation rather than at the distal end, with some larger individuals (Fig. 6A) showing small wedge-shaped plates nestled between larger sphenoids;

however, this needs to be confirmed through the study of more specimens.

The number of plates forming the ventral membrane remains more or less constant through growth. All specimens have between eight and twelve rows of infracentral plates, but there is no apparent relationship between the size of specimens and the number of plates. Plates that are added are inserted irregularly by intercalation, to judge from the distribution of the occasional much smaller elements nestled among larger ventral plates (Fig. 6B).

The relative length of food grooves remains constant throughout ontogeny, with the left food groove always extending to M1l and the right food groove to M2r. This is one of the most conservative characters in cinctans and thus taxonomically very important, as has been suggested in many previous studies (Ubaghs 1968; Friedrich 1993; Smith and Zamora 2009).

One significant change that does occur during ontogeny is the development of a ventral swelling on the anterior cinctus plates. Juveniles with a thecal length of 6 mm lack a ventral swelling (Fig. 6D), whereas it is always present in adults. It first appears in individuals about 12 mm in size and becomes progressively more prominent in larger individuals. In cinctans, ventral swellings are thought to have helped anchor the animal on the sediment surface (Ubaghs 1968, 1975) or raised the theca above the substrate (Zamora and Smith 2008), and hence their development in *Graciacystis* is likely an adaptation for an epibenthic suspension-feeding lifestyle (Friedrich 1993; Smith 2005; Zamora and Smith 2008). It is doubtful whether the lack of strong ventral swellings in juveniles indicates that they had a different ecology to adults; juvenile specimens occur in the same facies as adults, demonstrating that they lived in identical environmental conditions. Instead, as swellings are also weakly developed in immature specimens of *Gyrocystis testudiformis* (Friedrich 1993), their absence in juveniles probably reflects the plesiomorphic condition for cinctans (Smith and Zamora 2009).

The width of the infracentral integument increases at a considerably greater rate than the width of the marginal frame during ontogeny, indicating that cinctans enlarged the relative size of the lower integumentary surface. This is reflected by the very strong positive correlation between thecal width and the thecal width to marginal frame width ratio ($r = 0.979$, $p < 0.0001$; Fig. 8F). This is probably related to the increasing mass of the animal with age; enlarging the integumentary surface might have helped support the animal on soft substrates.

Based on the data presented earlier, cinctans appear to have been very conservative in their growth. Growth is largely achieved through the enlargement of plates that were formed early in ontogeny rather than by the addition of new plates, at least for the cinctus and stele. Plate addition appears to be more prevalent in the ventral and possibly dorsal integuments although plate growth remains predominant. Although we show the growth for just one species of cinctans, the fundamentally similar construction of other species points that all followed a similar growth strategy.

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REFERENCES

ÁLVARO, J. J., BAULUZ, B., PIERRE, C., SUBIAS, I. and VIZCAÏNO, D. 2008. Carbon chemostratigraphy of the Cambrian–Ordovician transition in a midlatitude mixed platform, Montagne Noire, France. *Geological Society of America Bulletin*, **120**, 962–975.

BRUGUIÈRE, J. G. 1791. *Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature, Contenant l'Helminthologie, ou les vers Infusoires, les vers Intestins, les vers Mollusques, etc., Volume 7*. Panckoucke, Paris, 180 pp.

FRIEDRICH, W. P. 1993. Systematik und Funktionsmorphologie mittelkambrischer Cincta (Carpoidea, Echinodermata). *Beringeria*, **7**, 3–190.

GOZALO, R., CHIRIVELLA MARTORELL, J. B., ESTEVE, J. and LIÑÁN, E. 2011. Correlation between the base of Drumian Stage and the base of middle Caesaraugustan Stage in the Iberian Chains (NE Spain). *Bulletin of Geosciences*, **86**, 545–554.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. *Paläontologische Zeitschrift*, **3**, 1–128.

JEFFERIES, R. P. S. 1990. The solute *Dendrocystoides scoticus* from the Upper Ordovician of Scotland and the ancestry of chordates and echinoderms. *Palaeontology*, **33**, 631–679.

KLEIN, J. T. 1734. *Naturalis dispositio Echinodermatum. Accessit lucubratiuncula de Aculeis Echinorum Marinorum, cum spicilegio de Belemnitis*. Schreiber, Gedani, 79 pp.

RAHMAN, I. A. and ZAMORA, S. 2009. The oldest cinctan carpoid (stem-group Echinodermata), and the evolution of the water vascular system. *Zoological Journal of the Linnean Society*, **157**, 420–432.

SAMANIEGO, A. H., ARAGONÉS, E., DEL OLMO, P., AGUILAR, M. and RAMÍREZ DEL POZO, J. 1972. Mapa geológico de España. E. 1: 50.000. Tabuenca (352). *Instituto Geológico y Minero de España*, 37 pp.

SMITH, A. B. 2005. The pre-radial history of echinoderms. *Geological Journal*, **40**, 255–280.

—— and ZAMORA, S. 2009. Rooting phylogenies of problematic fossil taxa; a case study using cinctans (stem-group echinoderms). *Palaeontology*, **52**, 803–821.

SWOFFORD, D. L. 2002. *PAUP* version 4.0b10 for Macintosh [computer program and documentation]*. Sinauer Associates, Sunderland, MA.

UBAGHS, G. 1968. Homostelea. S565–S581. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part S, Echinodemata*. Vol. 1 (2). Geological Society of America, Boulder, Colorado and University of Kansas Press, Lawrence, Kansas, 650 pp.

—— 1975. Early Palaeozoic echinoderms. *Reviews in Earth and Planetary Science*, **3**, 79–98.

ZAMORA, S. 2010. Middle Cambrian echinoderms from North Spain show echinoderms diversified earlier in Gondwana. *Geology*, **38**, 507–510.

—— 2011. Equinodermos del Cámbrico de España: situación actual de las investigaciones y perspectivas futuras. *Estudios Geológicos*, **67**, 59–81.

—— and ÁLVARO, J. J. 2010. Testing for a decline in diversity prior to extinction: Languedocian (latest Mid-Cambrian) distribution of Cinctans (Echinodermata) in the Iberian Chains, NE Spain. *Palaeontology*, **53**, 1349–1368.

—— and SMITH, A. B. 2008. A new Middle Cambrian stem-group echinoderm from Spain: palaeobiological implications of a highly asymmetric cinctan. *Acta Palaeontologica Polonica*, **53**, 207–220.

—— —— 2010. The oldest isorophid edrioasteroid (Echinodermata) and the evolution of attachment strategies in Cambrian edrioasteroids. *Acta Palaeontologica Polonica*, **55**, 487–494.

—— —— 2012. Cambrian stalked echinoderms show unexpected plasticity of arm construction. *Proceedings of the Royal Society of London, Series B*, **279**, 293–298.