

ROOTING PHYLOGENIES OF PROBLEMATIC FOSSIL TAXA; A CASE STUDY USING CINCTANS (STEM-GROUP ECHINODERMS)

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Abstract: Extinct clades whose higher-level relationships are problematic or disputed pose a particular problem for phylogenetic analysis because of the difficulty of establishing a convincing root. Cinctans are a problematic group of primitive preradiate echinoderms whose morphology is so distinct that few characters can be usefully homologized with any other group. Here we use a two stage approach, first constructing an unrooted network using the totality of phylogenetically informative characters in which individual plates are homologized, and then determining the root position with a much smaller set of recast characters that

can be polarized by outgroup and/or ontogenetic criteria. Furthermore, when rooting is based on stratigraphic criteria the same two major derived clades are identified, although basal relationships are somewhat different. We contend that the congruence of results obtained using our various approaches provides confidence that we have correctly rooted the cladogram. A revised taxonomy for Cincta is presented.

Key words: Stem group, echinoderms, cladistics, rooting, phylogenetic analysis, Cambrian, new taxa.

CLADISTIC analysis is a powerful means of determining relationships amongst taxa. Parsimony programs such as PAUP* (Swofford 2002) are very efficient at finding the shortest network connecting taxa on the basis of their observed traits, be they morphological or molecular. The most parsimonious network minimizes the number of character state changes across the entire topology and tells us about overall similarity of the taxa included. When character state changes are optimized over this network it is possible to differentiate homologous states from those that are homoplasious (i.e. those apparently identical states which arise in two or more parts of the network independently). However, networks are not very useful for biological sciences where we are often interested in the direction in which character state changes have occurred over time. To establish the polarity of traits and thus distinguish the primitive condition from the derived condition, the root of the cladogram needs to be identified. Furthermore, rooting a cladogram is the only way to distinguish between monophyletic and paraphyletic groups and thus establish the necessary framework for classification.

There are two widely accepted methods of rooting plus two additional *ad hoc* rules of thumb (Weston 1994). The most widely used method is outgroup polarization (e.g.

Maddison *et al.* 1984; Nixon and Carpenter 1993), whereby one or more closely related taxa that lie outside the group of interest are used to establish which character state is more general in its distribution and which more restricted. The assumption here is that character states shown by just some ingroup taxa, but not found within the wider ensemble, are derived. The more ingroup characters that can be polarized the more likely it is that the root position will be estimated accurately. Consequently, the outgroup method works best where a closely related taxon to the ingroup can be identified, as closely related taxa share the greatest number of characters that can be homologized unambiguously. Lundberg rooting, which uses an all zero outgroup, is another possibility but is difficult to implement where many characters are more complicated than simple presence/absence. For such characters the assignment of 0 and 1 to character states then becomes arbitrary.

A second method used for establishing character polarity, and thus root position, is through observing ontogenetic change (Wheeler 1990; Pinna 1994; Patterson 1994). If, during development, a character can be observed to change from one state to another, the assumption is that the earlier state is the more primitive and the later state represents an evolutionary elaboration. Again this method

is useful in extant groups where the complete development can be documented, but is rarely applied to fossil groups, where ontogenetic series are either incomplete or lacking altogether. A further difficulty arises where development has been truncated by paedomorphosis during evolution as paedomorphic forms will tend to be pulled down towards the root irrespective of their true position.

Thirdly the root position may be established by recourse to stratigraphic arguments and placed on the oldest known member of the ingroup (e.g. Fortey and Chatterton 1988). Here the assumption is made that the fossil record is relatively complete and preserves the representatives of the ingroup more or less in their correct order of evolutionary appearance.

Finally the root can be placed at midpoint in the network so as to minimize the average length between root and each terminal taxon, or, more simply, mid-length between the two most divergent taxa (Hess and De Moraes Russo 2007). This turns out to be largely consistent with rooting methods based on outgroup definition, but only when there is a strong phylogenetic signal. Where outgroup rooting generates an ambiguous or weakly supported root for the ingroup, midpoint rooting is less reliable (Hess and De Moraes Russo 2007). Furthermore, if the analysis is of fossil taxa rather than extant taxa, and those taxa are distributed at different distances in time from the basal node, then midpoint rooting is even more likely to generate misleading results.

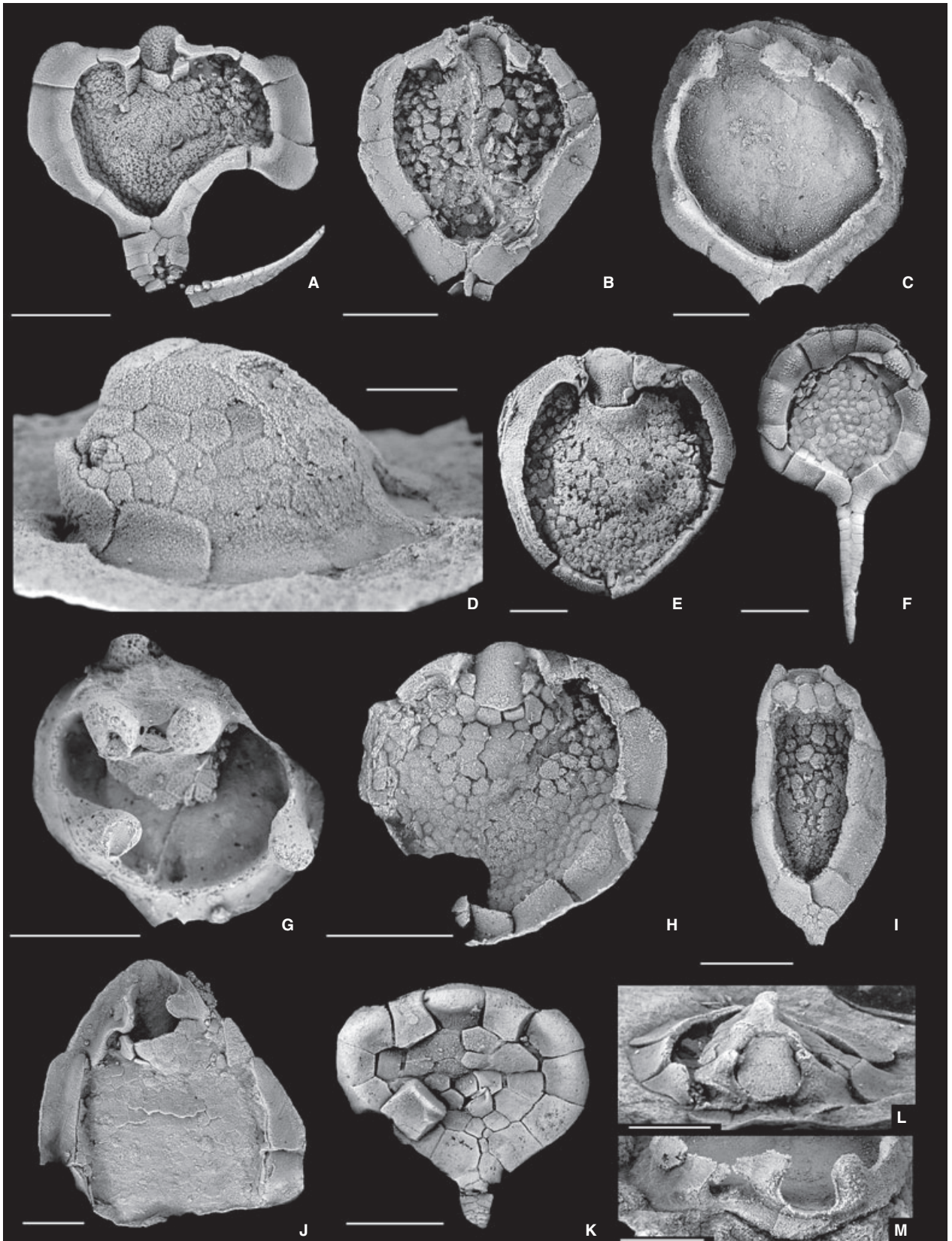
For many fossil groups the process of cladistic analysis is straightforward and the inclusion of a selection of closely related representatives from the sister taxon provides an appropriate means of rooting. In such cases the majority of characters that are informative for ingroup relationships can be observed in the outgroup(s) and thus polarized. However, problems arise where the fossil group in question is so morphologically derived compared to other taxa that selecting an outgroup is problematic. In such cases the vast majority of phylogenetically informative characters within the ingroup may simply have no obvious matching homologous structure in any outgroup. The extreme case is found when rooting the entire Tree of Life, where no outgroup exists. Here root placement

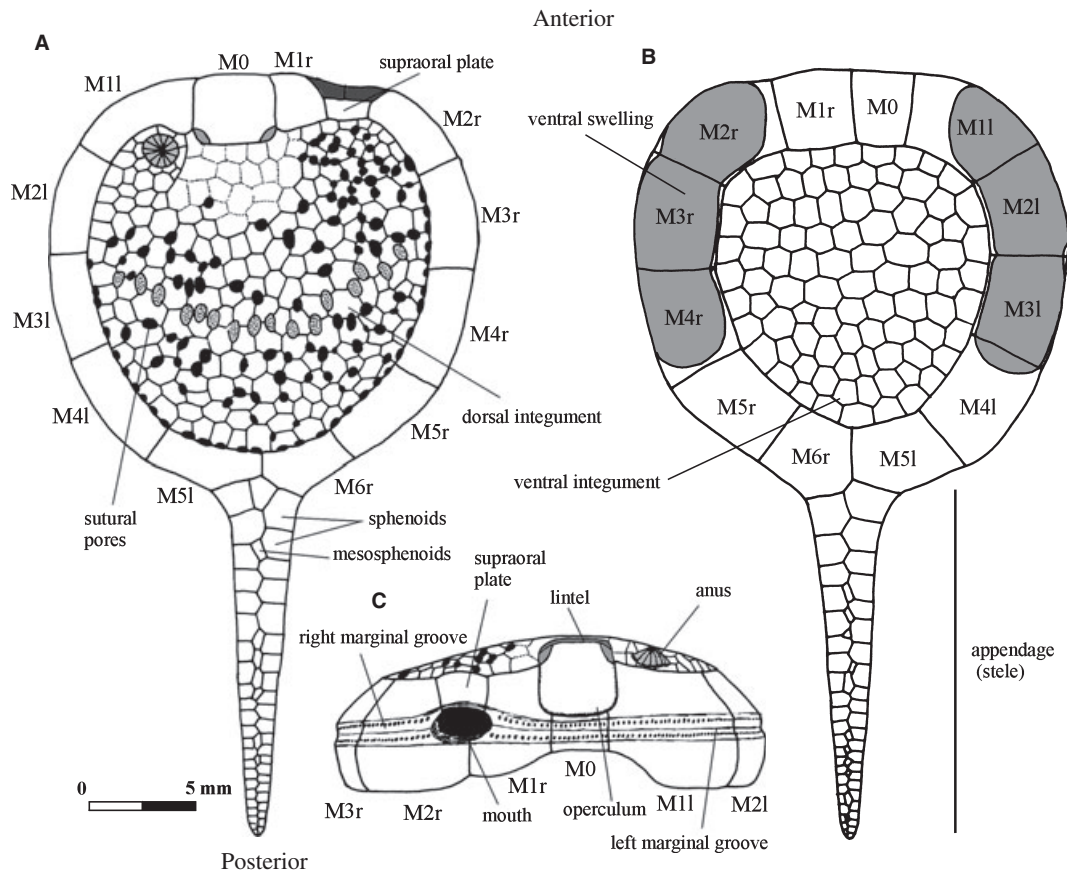
has been, and remains, highly controversial (Cavalier-Smith 2006; Lake *et al.* 2007), though analysis of the distribution of sequence gaps (indels) and other clearly derived sequence traits does allow certain groups to be recognized as nonbasal. In less extreme cases there may be an obvious, though morphologically highly differentiated, outgroup to use, as in the case of anomalocystitid mitrates (Ruta 1999b), where other mitrate groups provide an unambiguous outgroup for character polarization. With many highly problematic taxa, however, no obvious or agreed outgroup exists, and analysis of their phylogenetic relationships becomes difficult to implement. This is exactly the case we have with the Cincta.

Cinctans are an extinct group of benthic, calcite-plated echinoderms lacking radial symmetry. They are racquet-shaped with a near bilaterally symmetrical to strongly asymmetrical body or theca, and a posterior appendage or stele (Text-fig. 1). Their theca is framed by stout ossicles forming a rigid marginal ring (the cinctus). Within the cinctus dorsal and ventral plated integuments constructed of small tessellate plates enclose the body cavity. The cinctus is pierced by two openings at the anterior (Text-fig. 2). The larger opening is the more central and is covered by a large spoon-shaped plate called the operculum. The smaller lies to the right and, in almost all taxa, opens externally into left and right food grooves with their covering of small plates. These two grooves are usually unequally developed. At the posterior end is the stele, an appendage that is clearly bilaterally symmetrical and appears to arise as a direct continuation of the cinctus.

Barrande (1887) described the first cinctan from the Middle Cambrian of Bohemia. Because of their appendage and their calcite skeleton they were originally classified as pelmatozoan echinoderms. However, as they became better known, their unusual morphology and distinction from stemmed radiate echinoderms were recognized by both Jaekel (1900, 1918) and Bather (1913). A major advance in our knowledge of the group came when Ubaghs (1967) published his revision of cinctans in the Treatise on Invertebrate Palaeontology. At that time only four species in four genera of cinctans were known

TEXT-FIG. 1. A selection of different cinctan taxa. A, *Lignanicystis barriosensis* Zamora and Smith, 2008; dorsal view of the holotype MPZ 2007/776. B, *Asturicystis jaekeli* Sdzuy, 1993; dorsal view of the holotype PIW 93IX3/4. C, *Sucocystis undata* Friedrich, 1993; dorsal view of the holotype IGUR 1033a. D, *Gyrocystis testudiformis* Friedrich, 1993; lateral view of the holotype PIW 92V67. E, *Trochocystites bohemicus* Barrande, 1887; dorsal view of NMP 9060. F, *Trochocystites bohemicus* Barrande, 1887, ventral view of the lectotype NMP 9066. G, *Sucocystis quadricornuta* Friedrich, 1993; dorsal view of the holotype PIW 92V51. H, *Sotocinctus ubaghisi* Sdzuy, 1993; dorsal view of the holotype PIW 93IX1/1. I, *Gyrocystis badulesiensis* Friedrich, 1993; dorsal view of the holotype PIW 92V6I. J, *Progyrocystis disjuncta* Friedrich, 1993; dorsal view of the holotype PIW 92V56I. K, *Sucocystis theronensis* (Cabibel, Termier and Termier, 1959); ventral view of the specimen PIW 92V16I. L, *Gyrocystis testudiformis* Friedrich, 1993; frontal view of an adult specimen MPZ2008/4a. M, *Sucocystis undata* Friedrich, 1993; frontal view of the holotype IGUR 1033a. Scale bars all = 5 mm except D = 2 mm; L = 3 mm.





TEXT-FIG. 2. General drawing of a cinctan (*Trochocystites*) with major anatomical features indicated and marginal plates numbered. A, dorsal view. B, ventral view. C, anterior view.

(*Trochocystites*, *Trochocystoides*, *Gyrocystis* and *Decacytis*, the latter subsequently recognized as a junior synonym of *Gyrocystis*) and they were placed in their own class, the Homostelea. Ubaghs' careful work again emphasized just how different cinctans were from other carpoidea.

The next significant advance came with the monographs of Friedrich (1993) and Sdzuy (1993). Friedrich (1993) erected a large number of new species and genera, and provided high quality reconstructions and a wealth of anatomical data on the group. Using a hand-generated cladistic approach he presented a scheme of relationships within two speciose genera, *Gyrocystis* and *Sucocystis*. Sdzuy (1993) also established new taxa and considered phylogenetic relationships of the group, though without using any formal method. Ubaghs (1967), Friedrich (1993) and Sdzuy (1993) all recognized that a taxonomically important feature for the classification of cinctans related to the relative development of their food grooves. However, they did not agree as to how cinctans should be classified. Table 1 summarizes the competing classifications proposed by Friedrich (1993) and Sdzuy (1993) for the 17 and 20 species

known respectively at that time. Since then a further seven additional taxa have been proposed (Gil Cid and Domínguez 1995; Friedrich 1995; Fatka and Kordule 2001; Rozhnov 2006; Zamora and Smith 2008; Rahman and Zamora 2009).

Cinctans are confined to only a brief interval of time during the Middle Cambrian and were a component of benthic marine assemblages in Western Gondwana, Siberia and Avalonia (Barrande 1887; Termier and Termier 1973; Schröder 1973; Friedrich 1993, 1995; Sdzuy 1993; Fatka and Kordule 2001; Rozhnov 2006; Zamora and Smith 2008). Isolated plates of cinctans are very common in Middle Cambrian rocks but complete skeletons are preserved only under special conditions in specific echi-noderm Lagerstätten. For the most part cinctans are preserved as natural moulds covered with iron oxides and are best studied by making latex casts. A few species are preserved as recrystallized sparite calcite (e.g. Rozhnov 2006) and thus can be studied using modern imaging techniques (Rahman and Zamora 2009).

The strange and distinctive morphology of these animals has meant that cinctans have proved difficult to

TABLE 1. The competing classifications proposed by Friedrich (1993) and Szdzy (1993) for species of Cincta.

Classification of Friedrich (1993)	Classification of Szdzy (1993)
Family Trochocystitidae Jaekel, 1900	Family Trochocystitidae Jaekel, 1900
Genus <i>Trochocystites</i> Barrande, 1859	Genus <i>Trochocystites</i> Barrande, 1859
<i>Trochocystites bohemicus</i> Barrande, 1887	<i>Trochocystites bohemicus</i> Barrande, 1887
Genus <i>Trochocystoides</i> Jaekel, 1918	Genus <i>Trochocystoides</i> Jaekel, 1918
<i>Trochocystoides parvus</i> Jaekel, 1918	<i>Trochocystoides parvus</i> Jaekel, 1918
	<i>Trochocystoides planus</i> Szdzy, 1993
Family Sucocystidae Friedrich, 1993	Genus <i>Sucocystis</i> Cabibel <i>et al.</i> , 1959
Genus <i>Elliptocinctus</i> Termier and Termier, 1973	<i>Sucocystis theronensis</i> Cabibel, Termier and Termier, 1959
<i>Elliptocinctus barrandei</i> (Munier-Chalmas and Bergeron, 1889)	<i>Sucocystis bretoni</i> Friedrich, 1993
Genus <i>Sucocystis</i> Cabibel <i>et al.</i> , 1959	<i>Sucocystis undata</i> Friedrich, 1993
<i>Sucocystis theronensis</i> Cabibel, Termier and Termier, 1959	<i>Sucocystis melendezi</i> (Schröder 1973)
<i>Sucocystis bretoni</i> Friedrich, 1993	<i>Sucocystis acrofera</i> Friedrich, 1993
<i>Sucocystis undata</i> Friedrich, 1993	<i>Sucocystis quadricornuta</i> Friedrich, 1993
<i>Sucocystis melendezi</i> (Schröder 1973)	<i>Sucocystis ? maroccana</i> (Termier and Termier, 1973)
<i>Sucocystis acrofera</i> Friedrich, 1993	Genus <i>Sotocinctus</i> Szdzy, 1993
<i>Sucocystis quadricornuta</i> Friedrich, 1993	<i>Sotocinctus ubaghsi</i> Szdzy, 1993
<i>Sucocystis? maroccana</i> (Termier and Termier, 1973)	
Family Gyrocystidae Jaekel, 1918	Family Gyrocystidae Jaekel, 1918
Genus <i>Progyrocystis</i> Friedrich, 1993	Genus <i>Progyrocystis</i> Friedrich, 1993
<i>Progyrocystis disjuncta</i> Friedrich, 1993	<i>Progyrocystis disjuncta</i> Friedrich, 1993
Genus <i>Gyrocystis</i> Jaekel, 1918	Genus <i>Gyrocystis</i> Jaekel, 1918
<i>Gyrocystis platessa</i> Jaekel, 1918	<i>Gyrocystis platessa</i> Jaekel, 1918
<i>Gyrocystis testudiformis</i> Friedrich, 1993	<i>Gyrocystis testudiformis</i> Friedrich, 1993
<i>Gyrocystis badulesiensis</i> Friedrich, 1993	<i>Gyrocystis badulesiensis</i> Friedrich, 1993
<i>Gyrocystis erecta</i> Friedrich, 1993	<i>Gyrocystis erecta</i> Friedrich, 1993
	Genus <i>Elliptocinctus</i> Termier and Termier, 1973
	<i>Elliptocinctus barrandei</i> (Munier-Chalmas and Bergeron, 1889)
Family Uncertain	Genus <i>Asturicystis</i> Szdzy, 1993
Genus <i>Davidocinctus</i> Friedrich, 1993	<i>Asturicystis jaekeli</i> Szdzy, 1993
<i>Davidocinctus pembrokensis</i> Friedrich, 1993	
Genus <i>Ludwigicinctus</i> Friedrich, 1993	
<i>Ludwigicinctus truncatus</i> Friedrich, 1993	

place phylogenetically. They have been interpreted as (1) a basal group of hemichordates (Domínguez-Alonso and Jefferies 2005); (2) a derived group of blastozoans that have lost their radial symmetry (Sumrall 1997; David *et al.* 2000; Sumrall and Wray 2007); or (3) as primitive preradiate echinoderms (Ubaghs 1975; Smith 2005). This uncertainty over their position has arisen because surprisingly few of the anatomical features of cinctans can be homologized with structures in other crown group or stem-group echinoderms. The primary aim of this paper is not to investigate these wider relationships, however, but to generate the first rigorous cladistic analysis of cinctans and thus provide a framework within which to interpret their evolution. Our first step is to construct an unrooted network, which is relatively straightforward. More difficult, however, is establishing how to root this network.

MATERIALS AND METHODS

Taxa

Twenty-one species of cinctan were included in our cladistic analysis (Table 2). All species were studied first-hand from latex casts of original specimens drawn from collections housed in The Natural History Museum, London (NHM), Institut für Paläontologie der Julius-Maximilians-Universität Würzburg, Germany (PIW), Národní Muzeum, Prague, Czech Republic (NMP), Geologisch-Paläontologisches Institut, Universität Münster, Germany (GPM), Fachrichtung Geowissenschaften der Ernst-Moritz-Arndt-Universität Greifswald, Germany (FGWG) Institut de Géologie, Université de Rennes, France (IGUR), Museo Paleontológico, Universidad de Zaragoza, Spain (MPZ) and Instituto Geológico y Minero de España,

TABLE 2. The species of cinctan that are currently known.

Species	Stages	Locality and palaeocontinent	References
<i>Trochocystites bohemicus</i> Barrande, 1887	c.	Bohemia, Gondwana	Barrande (1887), Ubaghs (1967), Friedrich (1993)
<i>Trochocystoides parvus</i> Jaekel, 1918	c.	Bohemia, Gondwana	Jaekel (1918), Ubaghs (1967), Friedrich (1993)
<i>Trochocystoides planus</i> Szalay, 1993	Lower Caesaraugustan	Spain, Gondwana	Szalay (1993)
<i>Succocystis theronensis</i> Cabibel <i>et al.</i> , 1959	Lower-Middle Langued.	France, Gondwana	Cabibel <i>et al.</i> (1959), Friedrich (1993)
<i>Succocystis bretoni</i> Friedrich, 1993	Middle Languedocian	France, Gondwana	Friedrich (1993)
<i>Succocystis undata</i> Friedrich, 1993	Lower Languedocian	Morocco, Gondwana	Friedrich (1993)
<i>Succocystis melendezi</i> (Schröder, 1973)	Middle-?Upper Langued.	Spain, France?, Gondwana	Schröder (1973), Friedrich (1993)
<i>Succocystis acrofera</i> Friedrich, 1993	Middle Langued.	France, Gondwana	Friedrich (1993)
<i>Succocystis quadricornuta</i> Friedrich, 1993	Lower Langued.	Morocco, Gondwana	Friedrich (1993)
<i>Succocystis ? maroccana</i> (Termier and Termier, 1973)	–	Morocco, Gondwana	Termier and Termier (1973), Friedrich (1993)
<i>Sotocinctus ubaghsii</i> Szalay, 1993	Lower Caesaraugustan	Spain, Gondwana	Szalay (1993)
<i>Progrocystis disjuncta</i> Friedrich, 1993	Upp. Caes.-?Low. Langued.	Spain, Gondwana	Friedrich (1993)
<i>Gyrocyrtis platessa</i> Jaekel, 1918	Mid-Upp Caes, Low. Langued.	France, Spain, Gondwana	Jaekel (1918), Ubaghs (1967), Friedrich (1993)
<i>Gyrocyrtis testudiformis</i> Friedrich, 1993	Middle-Upper Caesaraugustan	Spain, Gondwana	Friedrich (1993)
<i>Gyrocyrtis badulesiensis</i> Friedrich, 1993	Upp. Caes.-?Low. Langued.	Spain, Gondwana	Friedrich (1993)
<i>Gyrocyrtis erecta</i> Friedrich, 1993	Upp. Caes.-?Low. Langued.	Spain, Gondwana	Friedrich (1993)
<i>Gyrocyrtis cruzae</i> Gil Cid and Domínguez, 1995	Upp. Caes.-?Low. Langued.	Spain, Gondwana	Gil Cid and Domínguez (1995), Friedrich (1995)
<i>Elliptocinctus barrandei</i> (Munier-Chalmas and Bergeron, 1889)	Lower-Middle Languedocian	France, Gondwana	Munier-Chalmas and Bergeron (1889), Ubaghs (1967), Friedrich (1993)
<i>Elliptocinctus vizainoi</i> Friedrich, 1995	–	Wales, Avalonia	Ubaghs (1967), Friedrich (1993)
<i>Davidocinctus pembrokensis</i> Friedrich, 1993	Upper Caesaraugustan	Wales, Avalonia	Friedrich (1995)
<i>Ludwigicinctus truncatus</i> Friedrich, 1993	Lower Languedocian	Germany, Gondwana	Friedrich (1993)
<i>Asturicyrtis jaekeli</i> Szalay, 1993	Lower Caesaraugustan	Spain, Gondwana	Friedrich (1993)
<i>Asturicyrtis havliceki</i> Fatka and Kordule, 2001	Upper Leon.-Lower Caes.	Bohemia, Gondwana	Szalay (1993)
<i>Nelegerocystis ivantzovi</i> Rozhnov, 2006	Lower-Middle Caes.	Russia, Siberia	Fatka and Kordule (2001)
<i>Rozanovicystis triangularis</i> Rozhnov, 2006	Lower-Middle Caes.	Russia, Siberia	Rozhnov (2006)
<i>Liganicyrtis barriosensis</i> Zamora and Smith, 2008	Lower Languedocian	Spain, Gondwana	Rozhnov (2006)
<i>Protocinctus manislaensis</i> Rahman and Zamora, 2009	Upper Leonian	Spain, Gondwana	Zamora and Smith (2008)
			Rahman and Zamora (2009)

Museo Geominero, Spain (MGM). All 21 species are represented by at least one reasonably complete and partially articulated specimen allowing the majority of their features to be scored. Two taxa could be scored for all 57 characters and a further four had less than 5% missing data. No taxon showed more than 37% missing data and the average missing entries for the 21 taxa is 10.6%. However, only a few are represented by large numbers of well-preserved specimens.

A further six species were initially scored but later rejected from the analysis as being too incompletely known. In all cases the quality of the material was poor, the illustrations and accompanying descriptions inadequate for our purposes, and original material was not available to us. These taxa are as follows.

Sucocystis? maroccana (Termier and Termier, 1973). Middle Cambrian of Morocco. This is based on only one poorly preserved specimen that is missing the supracentral integument, lintel and anterior part of the cinctus (see Friedrich 1993, pl. 15, fig. 1).

Davidocinctus pembrokensis Friedrich, 1993. Middle Cambrian of Wales. A single partially disarticulated and distorted specimen showing disrupted cinctus plates and lacking integuments and stele.

Asturicystis havliceki Fatka and Kordule, 2001. Middle Cambrian of the Czech Republic. The original description is based on several apparently well-preserved specimens. Unfortunately the original descriptions and illustrations provide little detail and we have not been able to borrow any material or latexes for study.

Nelegerocystis ivantzovi Rozhnov, 2006. Middle Cambrian of Siberia. The illustrated material is very poorly preserved and the skeleton appears to be recrystallized, obscuring or obliterating many important features. No material was available to us for study. This together with the inadequate description makes taxonomic comparison very difficult. However, *N. ivantzovi* has food grooves very similar in length to those of *Asturicystis jaekeli*. The shape of the theca, number of marginals and the absence of ventral swellings are identical in both genera, raising the possibility that they are synonymous.

Rozanovicystis triangularis Rozhnov, 2006. Middle Cambrian of Siberia. This taxon is the sole member of the family Rosanovicystidae characterized (according to Rozhnov 2006) by its triangular-shaped theca, eight marginals, and long food grooves encircling the entire theca. Unfortunately the material appears to be very poorly preserved, the description is inadequate, and it is impossible from the illustrations to confirm that there are eight marginal ossicles or even that food grooves are indeed present, let alone whether they run round the entire margin of the theca.

Trochocystoides planus Sdzuy, 1993. Middle Cambrian of northern Spain. This species was erected on the basis of a single specimen that comes from the same strati-

graphic level and the same locality as *Sotocinctus ubaghisi* Sdzuy, 1993 (Sdzuy 1993, p. 195). Both taxa were initially scored by us and proved to be identical in all morphological features save that there is one more marginal plate in the right side of the theca in *T. planus* than in *S. ubaghisi*. In other cinctans where we have access to numerous specimens from a single population (e. g. *Sucocystis theronensis*, *Elliptocinctus barrandei*, *Gyrocystis platessa*, *Trochocystites bohemicus*), we have observed that the number of marginals is not constant and can vary by one or rarely two plates on each side. Given that no other morphological differences exist, we here treat *T. planus* as a synonym of *S. ubaghisi*.

As outgroup we included the Middle Cambrian ctenocystoid *Ctenocystis*. However, only 12 of the original 57 characters could be scored in this taxon.

Plating nomenclature

For nomenclature of marginal plates we follow the system of Friedrich (1993). The anterior marginal plate that coincides with the axial plane and which underlies the operculum is M0 (Text-fig. 2). Marginal plates are then numbered successively around the margin towards the posterior appendage as M1r, M1l, M2r, M2l etc. with l and r indicating their position to the left or the right of the M0 plate in dorsal view. Important structures such as the adopercular processes and mouth are always found in the same position in different species and separated by an identical number of plates. This strongly suggests that individual plates forming the majority of the cinctus can be homologized amongst taxa. However, at the posterior the boundary between cinctus plates and appendage plates is more variable, as is the total number of plates forming the right and left sides of the cinctus. Indeed the stele appears to be a direct continuation of the cinctus, as first pointed out by Jefferies (1990). Unfortunately Ubaghs (1967) used a system of numbering cinctan plates starting from the appendage and working towards the anterior. This fails to capture the homology of the anterior and lateral plates and is thus not recommended.

Characters

A total of fifty-seven skeletal characters have been scored (Appendix). These included all characters given taxonomic significance in previous descriptions (primarily those of Ubaghs (1967), Friedrich (1993) and Sdzuy (1993)). Where possible characters were couched as presence/absence features referenced to specific homologous plates. For example, the homology of individual marginal plates is clear around the anterior and lateral part of the

cinctus amongst all cinctans (Text-fig. 2A; see below). We were therefore able to score whether food grooves are absent, present across part of, or present across the entire width of each individual marginal plate of the cinctus. A similar approach was taken when scoring for dorsal and ventral protuberances on the cinctus. The resultant data matrix (Appendix) has a total of 33 binary characters, 22 multistate characters and 2 invariant characters, giving a total of 126 character states. In addition we originally included a number of quantitative characters based on thecal dimensions and plate-plate ratios or angles. However, these proved to be highly variable between specimens of the same species, and highly prone to error due to postmortem distortion. Consequently, few were eventually included in the data matrix. We also excluded surface ornament characters, since these seemed to be highly dependent upon the nature of the enclosing sediment and reflected the quality of preservation rather than any original biological signal.

Almost half of all characters could be scored for all 21 taxa. Many of these relate to features of the cinctus, their food grooves, and the ventral plated integument. However, other anatomical features are preserved more rarely and remain unknown in a significant proportion of the taxa. Least well known are features of the stele, dorsal integument and the arrangement of food groove cover plates, all of which can be scored in less than 50% of the taxa. These show important taxonomic variation but, because they are so rarely preserved, it is currently impossible to determine at what level in the hierarchy these characters are informative.

For analyses that included an outgroup, we modified the matrix so as to avoid characters that required one-on-one homology between marginal frame plates and thus could not be applied to the outgroup. Characters 17–20 (presence or absence of dorsal nodes arising from specific marginal frame plate) were deleted and replaced by a simple presence/absence of dorsal nodes arising from the marginal ring. Characters 21–31 (presence/absence of ventral nodes on individual marginal plates) were similarly replaced by a single character; presence/absence of dorsal nodes arising from the marginal ring. Finally characters 46–53 (the presence of a food groove passing across individual plates of the marginal ring) were deleted and replaced by a single ordered character that captured the relative lengths of left and right food grooves. All three substituted characters could then be polarized by reference to our outgroup. This, however, reduced the data matrix to just 37 characters.

Analytical techniques

The data matrix was constructed using the computer program MacClade (Maddison and Maddison 2000) and

then analysed using PAUP* (Swofford 2002). Thirteen characters were treated as ordered, where there is a clear progression between three or more states (as for example in counts of the number of plates making up the left or right sides of the cinctus). All characters were initially treated as of equal weight. All analyses used the branch and bound search option, a method guaranteed to find the most parsimonious solutions. A first search was carried out on the full data matrix with just ingroup taxa. Tree robustness was tested using 1000 random addition bootstraps and by applying Bremer Decay. After the initial unweighted analysis a single reweighing of characters was carried out using the rescaled consistency index and a branch and bound search repeated. Tree stability was also explored by removing or including taxa with larger proportions of missing data. The entire process was repeated for the smaller data matrix with the outgroup included.

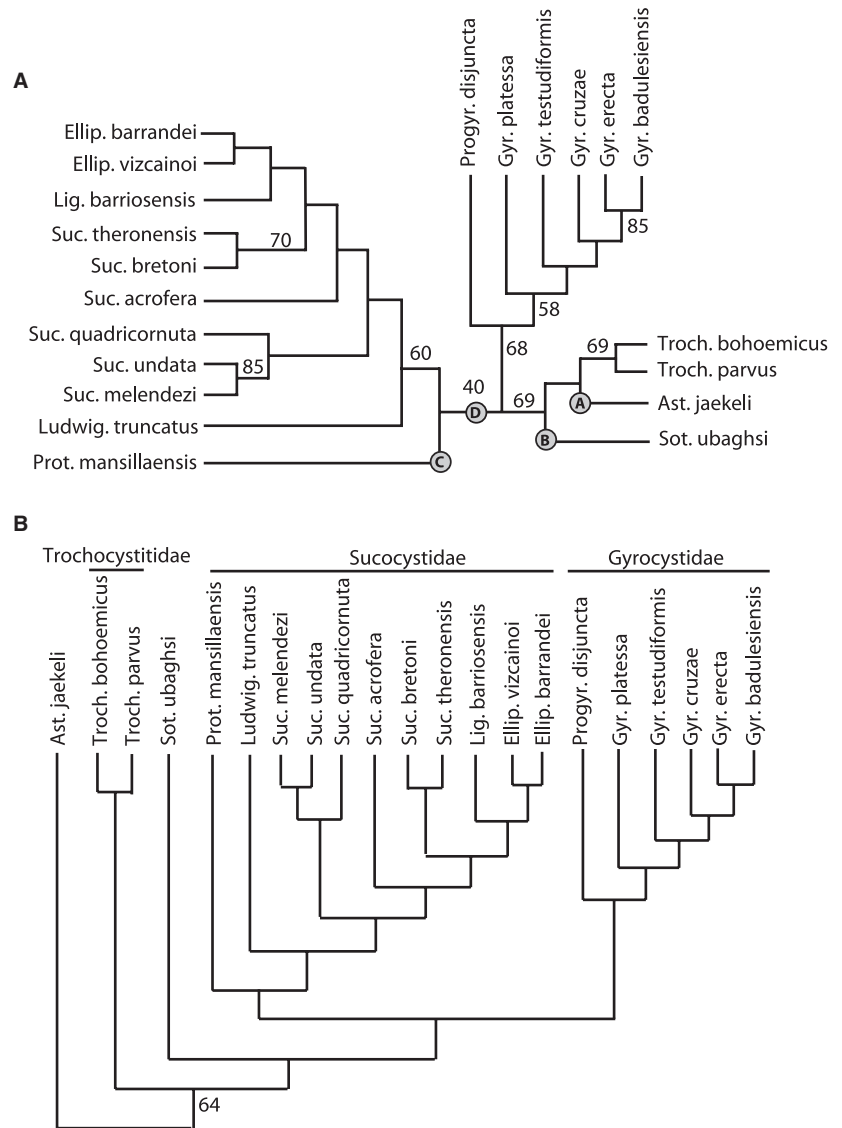
RESULTS

A branch and bound search of the data matrix found 120 equally most parsimonious trees of length 133 steps with a consistency index (CI) of 0.57, a retention index (RI) of 0.69 and a rescaled consistency (RC) index of 0.39. A majority rule consensus of these 120 trees is shown in Text-fig. 3A, which also indicates those branches that are absent in the strict consensus tree. The shortest tree in 10,000 randomized trees was, by contrast 186 steps long. After reweighing characters on their rescaled consistency index and rerunning the analysis we found just three trees, with a trichotomy joining (*Lignanicystis* + *Elliptocinctus*), (*Sucocystis theronensis* + *S. bretoni*) and *S. acrofera*. This was identical to the majority rule consensus of the unweighted trees. Support for most branches was, however, low (Text-fig. 3A).

Analysis of the modified data matrix of 37 characters with outgroup generated 21 trees length 88 steps, CI = 0.56, RI = 0.65, RC = 0.36, whose ingroup topology not surprisingly differed somewhat from that in the unrooted analysis. Bootstrap analysis supported a rooting between *Asturicystis* and other cinctans at 56% and there was Bremer support of just 1.

An evolutionary tree for cinctans was generated by superimposing the cladogram against the observed stratigraphical distribution of species (Text-fig. 4). Four species (*Gyrocystis erecta*, *G. badulesiensis*, *Elliptocinctus barrandei*, *Sucocystis undata*) lacked autapomorphies under accelerated transformation character optimization and could thus be treated as potential ancestors when constructing this evolutionary tree. However, only in one case was a plesiomorphic species (*Sucocystis undata*) stratigraphically older than its derived sister taxon (*S. melendezi*) and thus

TEXT-FIG. 3. Results of cladistic analysis. A, unrooted majority rule consensus of 120 equally most parsimonious trees using full data matrix, ingroup taxa only. Bootstrap values over 50% are shown at nodes. Filled circles = possible root positions. Heavy lines indicate branches and nodes that are present in the strict consensus of all 120 trees. Four possible root positions are indicated by grey circles as follows: A, outgroup rooting. A or B, ontogenetic rooting. C, stratigraphic rooting. D, mid-point rooting. B, semistrict consensus of the three cladograms found after reweighting characters by their rescaled consistency index. The root position is based on outgroup analysis. Bootstrap value for basal node based on reduced data matrix with *Ctenocystis* as outgroup.



potentially treated as two parts of a single anagenic lineage.

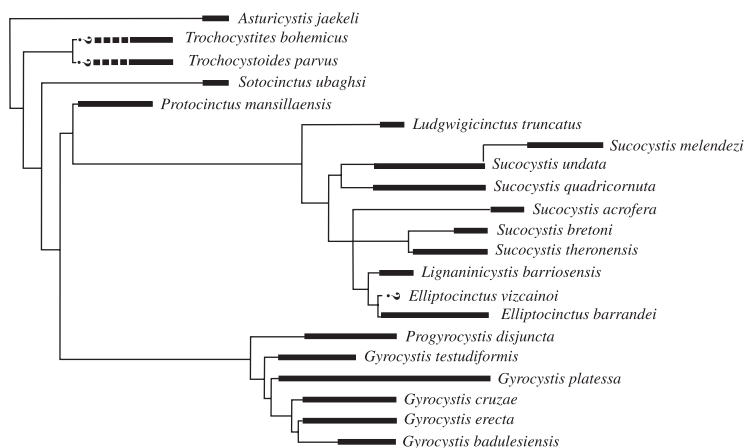
DISCUSSION

Rooting strategy

Cinctans are a highly distinctive group of echinoderms, and thus instantly recognizable. However, this distinctiveness also causes problems. Very few of the anatomical features that provide taxonomically informative variation amongst cinctan taxa can be found in other groups. For example, their appendage (stele) arises as a direct extension of the already highly differentiated cinctus plating and is clearly not homologous with the stem of a crinoid,

blastozoan or the stalk of a stylophoran, all of which form distinct morphological regions sharply differentiated from any framing body plates. The cinctan operculum also lacks apparent homologies. A few other echinoderms have a so-called opercular plate, the cornute *Juliaecarpus* (Ruta 1999a), the crinoid *Acolocrinus* (Sprinkle, 1982) or the solute *Dendrocystoides* (Caster, 1967; Jefferies 1990), but in all three cases these plates are totally different in construction and function and bear no close comparison with the articulated operculum of cinctans. Finally, cinctans are unique in the way their food grooves are constructed and arranged as a recumbent and asymmetric structure wrapped around the marginal framing plates. This is very different from the flexible, biserial flooring plates seen in crown group echinoderms. Indeed Ubagh's (1967, p. S566) lamented the fact that 'The Homostelea have

MIDDLE CAMBRIAN									Series
Series 3									Cambrian Stages and series proposed by the ICS
Stage 5			Drumian			Guzhangian			
Leonian			Caesaraugustan			Languedocian			Mediterranean Stages
Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper	



TEXT-FIG. 4. Cinctan evolutionary tree constructed by superimposing the cladogram of cinctan relationships against observed stratigraphical distribution (thick lines). One plesiomorphic metaspecies (*Sucocystis undata*) is treated as a potential ancestor to its derived sister taxon.

nothing in common with other ‘carpoids’ except the depressed form of their asymmetric body girdled by a marginal framework and their complete lack of radial symmetry’.

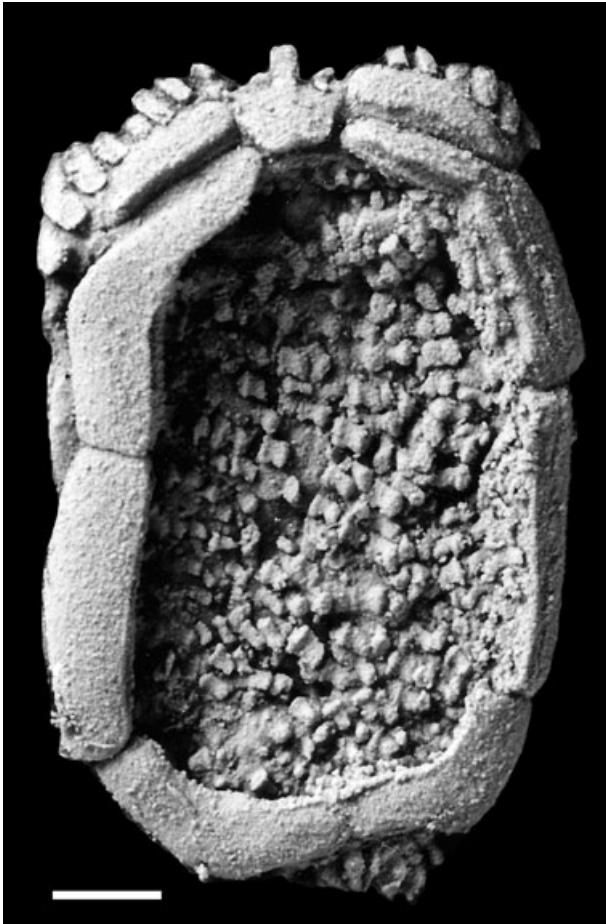
There are indeed very few undisputable homologies: the skeletal plates of cinctans are composed of calcite with a three-dimensional microstructure of stereom (Ubaghs 1967). This form of skeletal microstructure and its genomic basis are unique to echinoderms among living phyla (Bottjer *et al.* 2006) and provides a clear synapomorphy linking cinctans to the Echinodermata (Smith 2005). Cinctans also lack radial symmetry, one of the most prominent synapomorphies of crown group echinoderms, and so their sister group presumably lies amongst the other nonradiate stem-group echinoderms or beyond.

An analysis that includes only cinctans provides an unrooted network resolving the degree of morphological similarity amongst species, but it does not identify a direction of evolutionary change. For outgroup rooting, the best choice of taxon is the immediate sister group to the clade in question, as this generally displays the greatest number of homologous characters that can be polarized. However, the immediate sister group to cinctans is problematic. Ubaghs (1967) suggested that solutes were the sister taxon to cinctans, though without providing any justification for this statement. Friedrich (1993) believed closest comparison lay with the ctenocystoids. Jefferies *et al.* (1996) provided a cladistically justified argument that cinctans were the most primitive stem-group member of the Echinodermata, with ctenocystoids as the next branch off. This phylogenetic scenario was

also supported by Domínguez-Alonso (1999). David *et al.* (2000) provided a radically different interpretation, placing ctenocystoids as sister group to cinctans, but with both lying within a paraphyletic ‘eocrinoid’ group within blastozoan echinoderms. Sumrall (1997) and Sumrall and Wray (2007) recognized a clade of asymmetric echinoderms (Homalozoa) nested within Blastozoa in which solutes are placed as the most primitive, and cinctans are grouped as sister group to the clade (ctenocystoids + stylophorans). Smith (2005) could not determine a resolved position for cinctans, placing them in polytomy with stylophorans and solutes. However, he did not include ctenocystoids in his discussion. In summary, all agree that the immediate sister group to cinctans lies amongst the nonradiate echinoderms, and most workers place ctenocystoids in the immediate vicinity of cinctans, either in a slightly more or slightly less derived position.

Ctenocystoids have a superficial similarity to cinctans (Text-fig. 5). Both have a body plan consisting of a marginal frame of stout plates that enclose dorsal and ventral plated membranes, and in both the presumed mouth opens laterally through the marginal frame. Furthermore the mouth, although it lacks cinctan-type food grooves, is laterally extended to left and right forming the ctenoid organ (a series of small plates that overly and protect the large anterior opening). These have been tentatively homologized with food grooves (Sprinkle and Robison 1978, p. T1000; David *et al.* 2000).

However, when it comes down to a detailed comparison, it becomes much harder to recognize clearly homologous structures shared between ctenocystoids and



TEXT-FIG. 5. The ctenocystoid *Ctenocystis utahensis* Robison and Sprinkle, BMNH E63150, Middle Cambrian, Utah, USA. Scale bar = 1 mm.

cinctans, particularly those that are taxonomically important for cinctan phylogeny and classification. Ctenocystoids have no appendage, so all stele characters in cinctans remain unpolarized. The marginal frame in ctenocystoids is impossible to homologize in detail with that of cinctans. All ctenocystoids so far described in detail have a double ring of plates and the very different arrangement means that individual plates cannot be matched with those of cinctans. Whereas in cinctans the mouth opens between two plates (M1r and M2r) and there is a separate opening at the anterior covered by the operculum, in ctenocystoids there is only a single, wide opening that is framed by four marginal plates. As a consequence it is impossible to identify a single homologous plate in the marginal frame of ctenocystoids and cinctans. Domínguez-Alonso (1999) reported a ctenocystoid that has a single ring of marginals, but this is based on a single specimen that remains undescribed and individual plate homologies still cannot be made. The dorsal plated surface in ctenocystoids comprises a large number of

small polygonal plates as in some cinctans, but the ventral surface plating is very different in both the shape of the plates and in their organisation.

Nevertheless it is still possible to polarize a few characters by reference to the general body plan of ctenocystoids:

1. Overall symmetry (characters 1–3): ctenocystoids are more or less bilaterally symmetrical in outline whereas cinctans vary from almost bilaterally symmetric in outline to strongly asymmetric.
2. In the marginal ring we can score whether the ring is complete and for the number of plates forming a ring (characters 9–11) even though we cannot be sure of their exact homology. We can also score for their overall shape, since ctenocystoid marginal plates, whether a single or double row, are always flanged.
3. We can also score for the absence of projections from the marginal plates, both dorsal and ventral (characters 59, 60): absent in ctenocystoids, but present in some cinctans.
4. The dorsal plated membrane can be scored for two general characters, the presence or absence of epispines and the relative size of the plates making up the integument.
5. Finally we can score for overall ambulacral food groove asymmetry (character 58), even though we cannot score for the presence of food grooves on specific homologous plates as we have done for the main analysis. This ordered character measures the relative difference in length between left- and right-hand food grooves.

With these 11 characters polarized by reference to a ctenocystoid as outgroup, the ingroup topology is rooted between *Asturicystis* and the remaining cinctans. This, though small, is significantly more than can be obtained from selecting one of the other nonradiate echinoderm clades (stylophorans, solutes) as outgroup.

As a second, independent approach we turned to cinctan ontogeny to try to polarize the direction of evolution of certain character states. As all the taxa being compared are approximately similar in size and complexity paedomorphosis is not a complicating factor. This approach, however, is severely hampered by the dearth of information on cinctan development: few taxa are represented by abundant material and little study has been made of these. We were able to identify only two characters that could be polarized *a priori* using ontogenetic criteria: nodal development on the cinctus plates and marginal plate shape.

Swellings and projections on marginals are less well-developed in juveniles of *G. testudiformis* (Friedrich, 1993) and so are probably primitively absent. In populations of *S. quadricornuta* the dorsal swellings on the marginals are considerably smaller and less well-developed in small individuals and become more prominent in larger individuals. We therefore treat the absence of

dorsal swellings as primitive and the extremely developed processes as the most derived. The second character that can be polarized using ontogenetic information is the cross-sectional shape of the marginals. In *Gyrocystis platessa* the largest individuals have an extremely pronounced flange developed on marginal ossicles around the anterior margin, whereas in small individuals the flange is at best weakly developed.

The ontogenetic polarization criterion thus suggests that an absence of dorsal and ventral swellings and marginal ossicles without an anterior flange are all primitive states in cinctans. We can use these features to help narrow down a potential basal cinctan. Cinctans which lack as adults both dorsal and ventral nodes or swellings comprise *Progyrocystis*, *Sotocinctus*, *Asturicyctis* and *Gyrocystis platessa*. Of these *Gyrocystis* and *Progyrocystis* can be discounted as both have a well-developed anterior flange. Based on ontogenetic criteria therefore, we deduce that only *Sotocinctus* and *Asturicyctis* remain viable candidates as the most primitive known cinctan.

Stratigraphy is an *ad hoc* criterion for rooting a tree, but could conceivably be useful in groups with a long history and good fossil record. Unfortunately all cinctans come from a relatively short interval of time (the Middle Cambrian lasts only some 13 Ma; Gradstein *et al.* 2004). However, there is a group of distinctly older taxa of late Leonian – early Caesaraugustan age and a later cluster of late Caesaraugustan – Languedocian taxa (Text-fig. 4). The stratigraphically oldest cinctans known are *Protocinctus mansillaensis*, from the early Middle Cambrian (Leonian) of Spain (Rahman and Zamora, 2009), and ‘*Asturicyctis*’ *havliceki* from approximately the same horizon in Bohemia. ‘*A.*’ *havliceki* remains poorly known, but is unlikely to be a true *Asturicyctis* because its food groove pattern is very different, and it shows ventral swellings. It is probably a member of the Sucocystidae.

Also approximately contemporary are the two Bohemian taxa *Trochocystites* and *Trochocystoides*, while *Sotocinctus ubaghi* and *Asturicyctis jaekeli* appear just one zone higher in the early Middle Cambrian. This demonstrates that, even close to the start of the fossil record of cinctans, considerable morphological variation had already developed. Nevertheless, whether rooting is on *Protocinctus*, *Trochocystites*, *Trochocystoides*, *Asturicyctis* or *Sotocinctus*, two advanced clades are consistently present: a gyrocyctid clade, comprising (*Gyrocystis* + *Progyrocystis*) and a sucocystid clade comprising (*Ludwigicinctus* + *Sucocystis* + *Elliptocinctus* + *Lignanicystis*). What remains unclear, however, is the relationship of trochocystitids to these two groups, whether sister group to the sucocystids alone or sister group to the (sucocystids + gyrocyctids).

Finally the two morphologically most divergent taxa are *Trochocystites bohemicus* and *Gyrocystis platessa*, differ-

ing in 28 characters. When the midpoint of the ingroup network is used for rooting for ingroup taxa the root is placed between the clade comprising *Protocinctus*, *Progyrocystis* and *Gyrocystis* and the remainder (Text-fig. 3). This lies within the group of stratigraphically older taxa and close to other estimates of the root position.

In summary, our limited ontogenetic data identify two taxa (*Asturicyctis* and *Sotocinctus*) as more plesiomorphic than the remainder while outgroup rooting of our modified character–taxon matrix points to one of these (*Asturicyctis*) as sister taxon to all other cinctans. Although this is slightly younger than the stratigraphically oldest fossil cinctan, it does belong to the stratigraphically earlier cluster of taxa. All four rooting strategies, however, support the existence of two derived clades, the sucocystids and gyrocyctids. Given the close proximity in time of all cinctan species we are highly doubtful of the stratigraphic rooting criterion and take the congruence between outgroup and ontogenetic rooting as evidence for supporting *Asturicyctis* as the most primitive known cinctan.

Taxonomic outcomes

The cladistic analysis presented here provides the first rigorous phylogenetic analysis of the class, and includes all species based on reasonably complete material. If our identification of root position is correct, cinctans comprise three clades plus two basal taxa. There is strong support, irrespective of which rooting method is employed, for a clade Gyrocystidae that unites *Gyrocystis* and *Progyrocystis*. Five apomorphies support this group, though just two are unique, and the node has a bootstrap value of 67% and a Bremer Support of 1. Uncontested apomorphies for the clade relate to the development of the food grooves and the development of a broad flange on anterior marginal plates. In all Gyrocystidae the right food groove is missing and the left marginal groove extends only as far as plate M0. Grouping within the Gyrocystidae is exactly as suggested by Friedrich (1993), with *Progyrocystis* as sister group to a clade of *Gyrocystis* species, of which *G. platessa* is the most primitive. *G. platessa* differs from *G. testudiformis* and more derived forms in having: (1) a more symmetrical shape, (2) dorsal and ventral plating more similar in development, and (3) in primitively lacking a ventral node on plate M0.

A second major clade comprises the taxa *Protocinctus*, *Ludwigicinctus*, *Sucocystis*, *Lignanicystis* and *Elliptocinctus*. This grouping is supported by eight apomorphies, of which two occur nowhere else and relate to the left food groove extending only as far as plate M11. Bootstrap support for this node is, however, only 37% and the clade collapses in trees just one step longer. At the base of this clade lies *Protocinctus*, the oldest cinctan known. More

derived members of this clade are characterized by a rather distinctive ventral pattern of nodes on their marginal plates, and in having six rather than five plates from M0 to posterior closure of ring on the right-hand side of the cinctus. Bootstrap support for this node is stronger at 61% and there is a Bremer Support of 1.

Ludwigicinctus was not included in any family by Friedrich (1993) but in our cladistic analysis it is the next most primitive member of this clade. Friedrich (1993, text-fig. 21e) reconstructed it as having a very short food groove that does not even reach as far as plate M0. But his photograph of the holotype (Friedrich 1993, plate 24 fig. 1c) clearly shows the left food groove extending as far as plate M11, exactly as in some *Sucocystis* species such as *S. theronensis*. Two character state changes separate *Ludwigicinctus* from *Sucocystis*, the development of a continuous ventral swelling rather than a single node-like swelling on plate M0 ventrally, the overall similarity in size of plates forming the ventral integument, In other features (e.g. number and size of infracentral plates, shape of the theca, absence of suropercular processes, food groove development) *Ludwigicinctus* is very close to *Sucocystis*.

Sucocystis, in our analysis, forms a paraphyletic grade below a small clade comprising *Elliptocinctus* and *Lignanicystis*. All species are broadly similar, distinguished primarily by small differences in the relative length of the right-hand food groove and the distribution of ventral swellings on the marginal ring. There are two well-supported clades: one pairing *S. undata* and *S. melendezi* and the other uniting *S. theronensis* and *S. bretoni*. *S. undata* and *S. melendezi* differ only in the overall shape of the theca (wider than long in *S. melendezi*, approximately as wide as long in *S. undata*). This pairing is supported by 85% bootstrap and a Bremer decay index of 2. Whether this minor difference in shape justifies separation is doubtful. However, there are additional distinguishing features: *S. undata* has marginal plates that are thicker, and its cinctus is lower than in *S. melendezi* and so the two species are maintained. *S. quadricornuta* is sister group to these two taxa, all three species having dorsal swellings developed on the same four homologous marginal plates.

The other pairing which links *S. theronensis* and *S. bretoni*, is supported by a 71% bootstrap value. These two taxa are more obviously differentiated, with *S. theronensis* having a prominent spine developed on the central plate of its lintel, which is missing from all other species. The type species of *Sucocystis* is *S. theronensis* Cabibel, Termier and Termier, 1959 and so, to have only monophyletic clades, we propose to separate *S. undata*, *S. melendezi*, and *S. quadricornuta* into a new genus, *Undatacinctus*, type species *Sucocystis undata* Friedrich, 1993.

Elliptocinctus and *Lignanicystis* form a derived clade within the *Sucocystis sensu lato* clade based on the shared

presence of two apomorphies: the marginal plates forming the lateral part of the cinctus have a well-developed lateral flange, and the dorsal projections developed on marginal M1l and M1r are directed anteriorly rather than vertically (character 35). *Elliptocinctus* can be easily distinguished from *Sucocystis* by its well-developed suropercular processes, which project strongly (character 33: convergent with some *Gyrocystis*).

Lignanicystis was originally placed within Trochocystitidae (Zamora and Smith 2008) as it shares one obvious synapomorphy with *Trochocystites*, namely a row of sutural pores piercing the dorsal membrane. However, this character can only be determined in exceptionally well-preserved specimens, and cannot be scored in the majority of cinctans, including all species of *Sucocystis*. Its distribution may be more general than current knowledge suggests. Against this, *Lignanicystis* shares an identical food groove arrangement and pattern of ventral nodes on the cinctus with both *Sucocystis* and *Elliptocinctus*. *Lignanicystis* is easily separated from both *Sucocystis* and *Elliptocinctus* by a suite of distinctive features, such as its hatchet-shaped M4 plates, its bridge-like M5r plate and its strongly asymmetric theca.

Trochocystites and *Trochocystoides* form a clade with 70% bootstrap support and a Bremer decay index of 1. Eight apomorphies unite these two taxa, but only two are unique, again relating to the relative development of the food groove, which in these taxa extends to M4r and M3l. *Trochocystites* is the type species of the family Trochocystitidae and this name can be applied to unit these two genera.

Sotocinctus remains outside the three clades so far discussed, more derived than Trochocystitidae but sister group to the Gyrocystidae and Sucocystidae combined (Text-fig. 3B). It primitively lacks ventral swellings and

TABLE 3. Recommended classification of Cincta following our cladistic analysis and the conventions of Wiley (1979).

Plesion (Class) Cincta Jaekel, 1918
Genus <i>Asturicystis</i> Sdzuy, 1993
Genus <i>Sotocinctus</i> Sdzuy, 1993
Family Trochocystitidae Jaekel, 1918
Genus <i>Trochocystites</i> Barrande, 1859
Genus <i>Trochocystoides</i> Jaekel, 1918
Family Sucocystidae Friedrich, 1993
Genus <i>Protocinctus</i> Raman and Zamora, 2009
Genus <i>Ludwigicinctus</i> Friedrich, 1993
Genus <i>Undatacinctus</i> nov.
Genus <i>Sucocystis</i> Cabibel, Termier and Termier, 1959
Genus <i>Elliptocinctus</i> Termier and Termier, 1973
Genus <i>Lignanicystis</i> Zamora and Smith, 2008
Family Gyrocystidae Jaekel, 1918
Genus <i>Progyrocystis</i> Friedrich, 1993
Genus <i>Gyrocystis</i> Jaekel, 1918

has food grooves that are intermediate in length between those of *Asturicystis* and the Trochocystitidae on the one hand, and the short food grooves of Gyrocystidae and Sucocystidae. A revised classification for the Cincta is given in Table 3.

SYSTEMATIC PALAEOLOGY

Family SUCOCYSTIDAE Friedrich, 1993

Genus UNDATAINCTUS gen. nov.

Type species. *Sucocystis undata* Friedrich, 1993, p. 84.

Other species included. *S. melendezi* (Schröder, 1973) and *S. quadricornuta* Friedrich, 1993.

Occurrence. Middle Cambrian (Languedocian) of Spain and Morocco and possibly also in the Languedocian of France.

Diagnosis. A clade of Sucocystidae with the following synapomorphy: obvious protuberance developed on the dorsal part of plates M2l, M3l, M3r and M4r. Other (plesiomorphic) features: protuberances present on ventral surface of marginal ring – always present on plates M0, M2l, M3l, M2r, M3r and M4r. Food groove with short right-hand branch extending only as far as plate M2r and left-hand branch extending to plate M1l. Ventral plated surface composed of relatively few large plates.

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APPENDIX

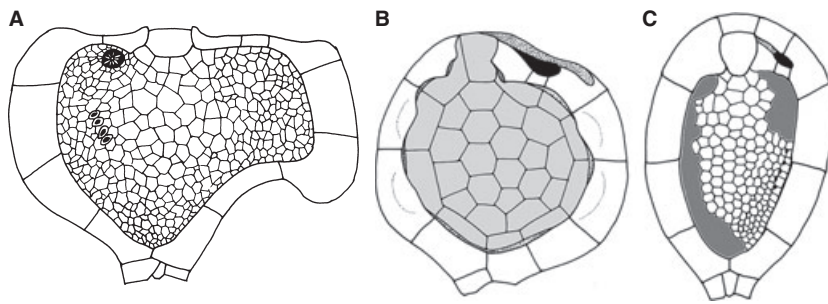
List of characters and character states used in the phylogenetic analysis of Cincta, and data matrix. Characters 1–57 are used for analysis of ingroup taxa only, characters 1–16, 32–45 and 54–60 are used for analysis with outgroup.

General features

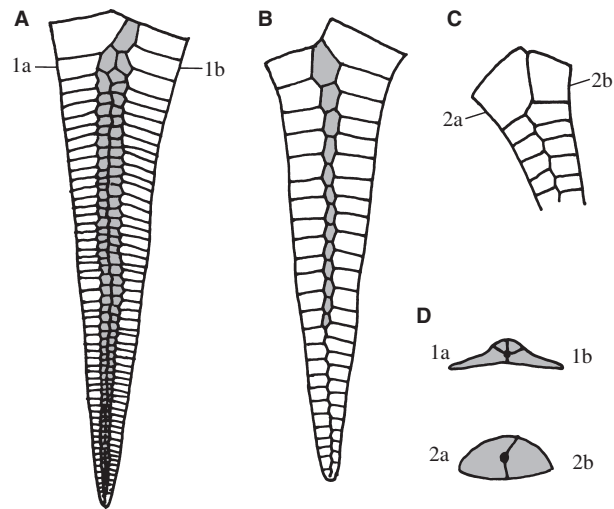
1. Symmetry of body: bilaterally symmetrical in outline (cinctan Lwidth/Rwidth >0.9) (0: Text-fig. 6C); slightly asymmetric (Lwidth/Rwidth <0.9, >0.75) (1: Text-fig. 6B), strongly asym-

metric, with obvious posterior right embayment (Lwidth/Rwidth <0.75) (2: Text-fig. 6A). Body asymmetry was measured by taking a line from the point of stele attachment to the centre of marginal plate M0 and measuring maximum distance to the edge of the cinctus to both left (Lwidth) and right (Rwidth) of this line (Text-fig. 2). The ratio of these two measurements provides a metric for how asymmetric the body is in outline.

2. Shape: subcircular theca approximately as wide as long (0: Text-fig. 6B); ovate theca much narrower than long (1: Text-fig. 6C) Theca widest proximally and tapering



TEXT-FIG. 6. A, *Lignanicystis barriosensis*, dorsal view (after Zamora and Smith 2008). B, *Sucocystis undata*, dorsal view (modified from Friedrich 1993). C, *Gyrocystis platessa*, dorsal view (from Friedrich 1993). Dark grey shading = missing areas; light grey shading = internal parts where supracentral integument is unknown. Dorsal surface of *S. undata* unknown.



TEXT-FIG. 7. Dorsal views of steles with mesosphenoids shaded (A, B, C) and cross-sections of steles (D, E). A, *Lignanicystis barriosensis* (after Zamora and Smith 2008). B, *Sucocystis theronensis* (from Friedrich 1993). C, *Trochocystoides parvus* (from Friedrich 1993).

towards appendage (2: Text-fig. 1B) wider than long (3: Text-fig. 6A).

3. Anterior margin: rounded (0: Text-fig. 6C), straight, horizontal (1: Text-fig. 6A).

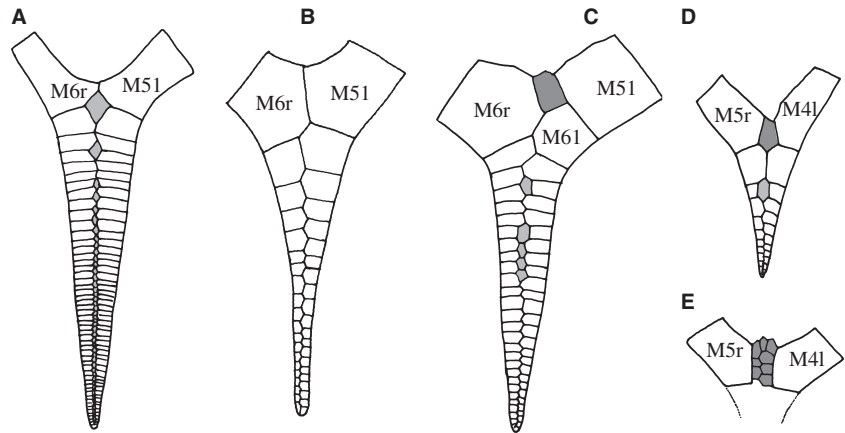
Stele

4. Cross-sectional shape immediately below theca (Text-fig. 7D): ovate (0); lozenge-shaped (1).
5. Length of stele in proportion to body: greater than half the length of the cinctus (0); shorter than half the length of the cinctus (1).
6. Mesosphenoid plates on dorsal surface: absent proximally (0: Text-fig. 7C); present proximally (1: Text-fig. 7A, B).
7. Mesosphenoidal plates on dorsal surface biserially arranged distally (Text-fig. 7A): no (0); yes (1).
8. Mesosphenoidal plates on ventral surface (Text-fig. 8A–C): absent (0); a few scattered plates about mid-length (1); present throughout forming a near continuous series (2).

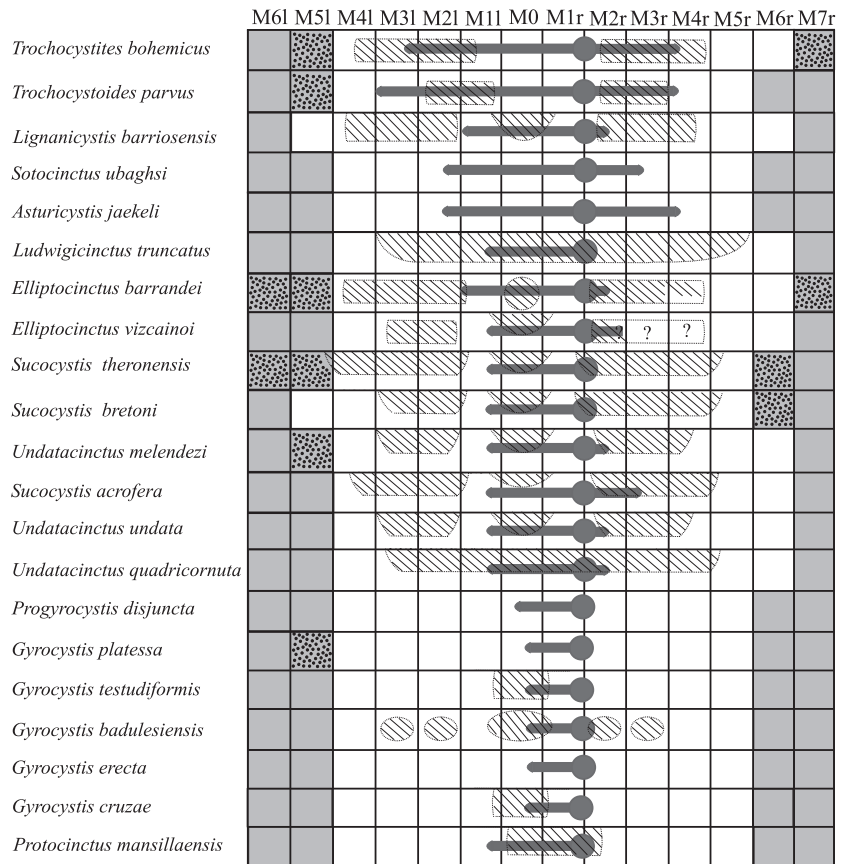
Marginal frame (for pattern of ventral nodes developed around cinctus and number of marginals see Text-fig. 9)

9. Posterior marginal plate arrangement: marginal plates abut forming a continuous circlet (0: Text-fig. 8B); marginal plates separated at posterior extremity by intercalated plates extending in from the ventral plated membrane (1: Text-fig. 8E); left and right marginal plates separated by one infracentral plate (2) (Text-fig. 8D, 9).
10. Number of marginal plates between M0 and the posterior closure of the ring around the right-hand side of the cinctus: five plates (0); six plates (1); seven plates (2) [ordered].
11. Number of marginal plates between M0 and the posterior closure of the ring around the left-hand side of the cinctus: four plates (0); five plates (1); six or seven plates (2) [ordered].
12. Anterior margin of plate M0; vertical or rounded (0: Text-fig. 10 – *Sucocystis*); projecting as a strong flange (1: Text-fig. 10 – *Gyrocystis*).
13. Shape of marginal plates forming lateral part of cinctus: wedge-shaped with lateral flange (0: Text-fig. 1A); without lateral flange (1: Text-fig. 1G) rounded in external section (2: Text-fig. 1E).
14. Interior dorsal edge of marginal plates: smooth (0); corrugated (1).
15. Plate M2r exsert from ring, not reaching plated dorsal or ventral integuments: no (0: Text-fig. 11A); yes (1: Text-fig. 11C).
16. Plate M4 hatchet-shaped: no (0: Text-fig. 6C); yes (1: Text-fig. 6A).
17. Protuberance on the dorsal part of plate M2l (Text-fig. 10): absent (0); present (1).
18. Protuberance on the dorsal part of plate M3l (Text-fig. 10): absent (0); small node (1); large projecting spike (2) [ordered].
19. Protuberance on the dorsal part of plate M3r (Text-fig. 10): absent (0); present (1).
20. Protuberance on the dorsal part of plate M4r (Text-fig. 10): absent (0); small node (1); large projecting spike (2) [ordered].
21. Protuberance on the ventral part of plate M5l: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).
22. Protuberance on the ventral part of plate M4l: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).

TEXT-FIG. 8. Proximal steles and posterior side of the cinctus in ventral view. A, *Lignanicystis barriosensis* (after Zamora and Smith 2008). B, *Elliptocinctus barrandei* (from Friedrich 1993). C, *Sucocystis theronensis* (from Friedrich 1993). D, *Protocinctus mansillaensis*. E, *Progyrocystis disjuncta*. Dark grey shading = intercalated plates in the posterior side of the cinctus; light grey shading = mesosphenoids.

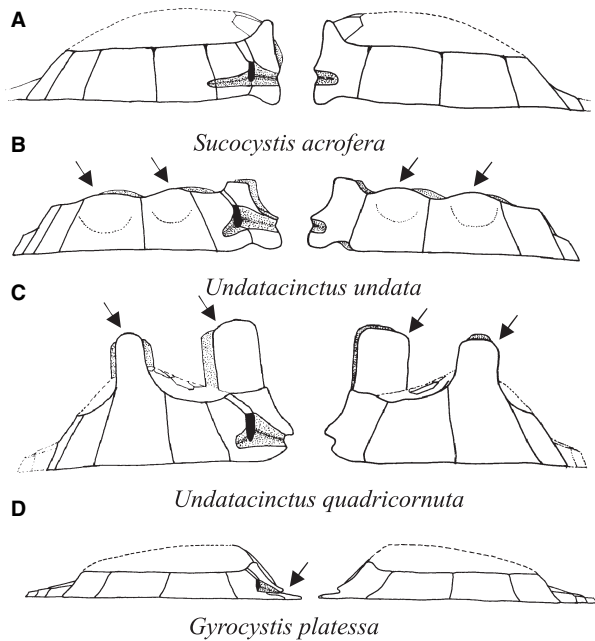


TEXT-FIG. 9. Schematic summary of number of marginal plates in the cinctus, food groove distribution and ventral swelling development on marginal plates for all species included in the analysis. M1–M7 marginal plates; l = left, r = right; open boxes = marginal plate present; grey circle = position of mouth; thick grey line = extent of left or right food groove; oblique hatching = presence of ventral swelling on marginal plate, grey boxes with dots = marginal plate sometimes present.



- 23. Protuberance on the ventral part of plate M3l: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).
- 24. Protuberance on the ventral part of plate M2l: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).
- 25. Protuberance on the ventral part of plate M1l: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).
- 26. Protuberance on the ventral part of plate M0: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).

- 27. Protuberance on the ventral part of plate M1r: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).
- 28. Protuberance on the ventral part of plate M2r: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).
- 29. Protuberance on the ventral part of plate M3r: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).
- 30. Protuberance on the ventral part of plate M4r: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).



TEXT-FIG. 10. Lateral views of various species showing the relative development of dorsal projections on marginals and anterior margin of M0 in profile.

31. Protuberance on the ventral part of plate M5r: absent (0); present forming an isolated mound (1); present forming part of a continuous ridge with contiguous plates (2).
32. Shape of plate M2: uniform, trapezoidal with rounded outer edge (0: Text-fig. 6C); distinctly angled (1: Text-fig. 6A).

Operculum and porta

33. Marginal plates 1l and 1r with strong dorsal projections extending beyond the articulation facet with the superoperculars (Text-fig. 12): no (0); yes but small (1); yes as very large peg-like spike (2) [ordered].
34. Marginal plates 1l and 1r with thin, plate-like dorsal flanges: no (0); yes (1: Text-fig. 1J).
35. Projections from marginal plates M1l and M1r: more or less vertically oriented (0); directed towards the anterior (1).
36. Suropercular facet on plates M1l and M1r: rudimentary or absent (0: (Text-fig. 1B, H); forming an obvious flat triangular zone (1: Text-fig. 1A, C).

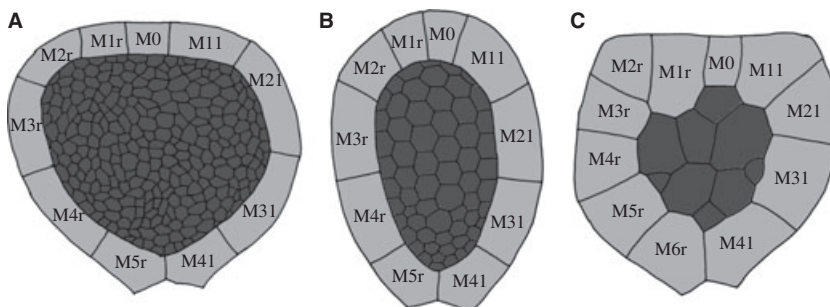
37. Number of plates forming dorsal margin of operculum (Text-fig. 12): 6–7 (0); 5 (1); 3 or 4 (2) [ordered].
38. Central plate of lintel with protuberance or spine: no (0); yes (1).

Dorsal and ventral membranes

39. Sutural epispires on dorsal surface: absent (0); present as arc on left-hand side (1: Text-fig. 6A); present scattered on right-hand side (2: Text-fig. 6C);
40. Dorsal surface: uniform ornament and plating (0: Text-fig. 1H); with distinct anterior and marginal zones differentiated in plate shape and ornament (1: Text-fig. 1A).
41. Ventral plated surface composed of: only a few very large plates (0: Text-fig. 11C); between 40–75 plates (1: Text-fig. 11B); a large number of small, uniform plates (2: Text-fig. 11A) [ordered].
42. Ventral plates distinctly larger than dorsal plates: no (0); yes (1).
43. Ventral swellings developed on anterior infracentral plates: no (0); yes.
44. Very large, differentiated ventral infracentrals in anterior region: no (0); yes (1).
45. Dorsal tegmen swollen centrally (Text-fig. 1D): no (0); yes (1).

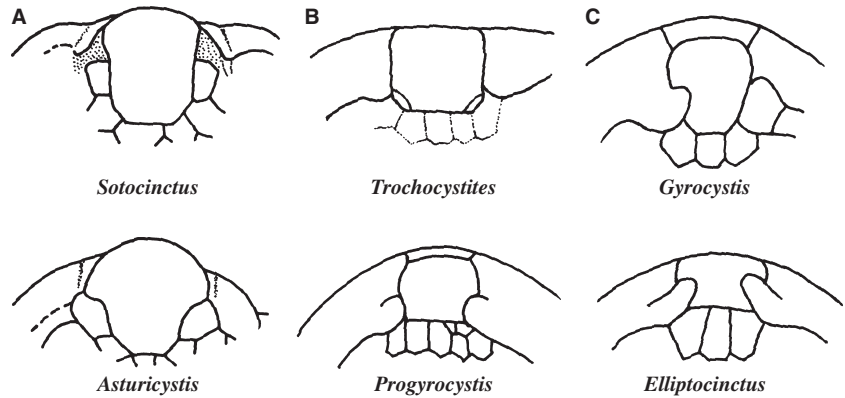
Food grooves (for pattern of food grooves development see Text-fig. 9)

46. Plate M3l – food groove: absent (0); extends onto plate but does not cross (1); extends across entire plate (2) [ordered] Text-fig. 9).
47. Plate M2l – food groove: absent (0); extends onto plate but does not cross (1); extends across entire plate (2) [ordered].
48. Plate M1l – food groove on plate: absent (0); extends onto plate but does not cross (1); extends across entire plate (2) [ordered].
49. Plate M0 – food groove on plate: absent (0); extends onto plate but does not cross (1); extends across entire plate (2) [ordered].
50. Plate M1r – food groove on plate: absent (0); extends onto plate but does not cross (1); extends across entire plate (2) [ordered].



TEXT-FIG. 11. Ventral views. A, *Sotocinctus ubaghsi*. B, *Gyrocystis platessa* (from Friedrich 1993). C, *Ludwigincinctus truncatus* (from Friedrich 1993). Dark grey shading = infracentral integument; light grey shading = marginals.

TEXT-FIG. 12. Schematic diagrams of plating associated with the dorsal porta-operculum complex for different genera of cinctans.



- 51. Plate M2r – food groove on plate: absent (0); extends onto plate but does not cross (1); extends across entire plate (2) [ordered].
- 52. Plate M3r – food groove on plate: absent (0); extends onto plate but does not cross (1); extends across entire plate (2) [ordered].
- 53. Plate M4r – food groove on plate: absent (0); extends onto plate but does not cross (1); extends across entire plate (2) [ordered].
- 54. Upper and lower rim of food groove with distinct pits: no (0); yes (1).
- 55. Position of food groove as it passes around anterior of cinctus: below ambitus and facing downwards (0); at ambitus and facing forwards (1).
- 56. Path of left food groove as it crosses plate M0: distinctly curved ventrally (0: Text-fig. 1M); more or less straight (1).
- 57. Construction of plated membranes covering food groove: upper and lower sheets of multiple small elements (0); an upper and lower biseries of plates (1).

Additional characters added when outgroup is included and after removal of characters 17–31 and 46–53.

- 58. Relative lengths of left- and right-hand food grooves: symmetric left and right food grooves extending the same number of marginal plates away from the mouth (0); asymmetric with left-hand food groove extending no more than 1 plate further than the right-hand food groove (1); asymmetric with left-hand food groove extended by 2 or more plates further than the right-hand food groove (2); asymmetric, right-hand food groove completely absent (3) [ordered].
- 59. Marginal ossicles: smooth and flat ventrally (0); with distinct ventral swellings on at least some plates (1).
- 60. Marginal ossicles: smoothly rounded dorsally (0); with distinct node or spike on at least some plates (1).

Data matrix (a = 0&1; b = 1&2; c = 0&1&2; d = 0&3;- = inapplicable).

Gyro_plates	1101110100	a100000000	-000000000	0010012020	1100000012	00001-1300
Gyro_test	0001111100	0100000000	-000010000	0010012020	1011100012	00001-1310
Gyro_cruz	1001?10?00	0100000000	??00010000	0010012???	0?00?00012	00001-?310
Gyro_badul	1101110200	0110000000	-011010110	00201120?0	0100000012	00001-1310
Gyro_erecta	110?????00	0110000000	-?????????	?0201120??	?????000012	00001-?3?0
Progyro_disj	010?????10	0100000000	-000000000	0001001000	2000000012	00001-0300
Proto_mans	010111??20	0010000000	-002220000	0000-120??	2000?0?122	000011?310
Ellip_barran	aa0111010b	c000000000	0222010222	00201120?0	1100000122	100011?210
Ellip_vizcan	0100?0??01	00?1000000	-0220102??	00201120?0	0100000122	1?001??210
Suco_ther	130111011a	c010000000	0222010222	00100121??	0100000122	000011?310
Suco_breton	13011??111	a010000000	0022010222	00100120??	0100000122	000111?310
Lignan_barrio	1311011201	1000010000	0222010222	0110112011	2000000122	100000?210
Suco_undata	100?????01	0010001111	-022010222	0000-1????	0?00?00122	100010?211
Suco_acrofe	230?????01	0010000000	-022010222	00100120??	0100000122	2100110110
Suco_quad	100?????01	0010000202	-022222222	0000-120??	0100000122	100001?211
Suco_melen	130?????01	0010001111	-022010222	0000-120??	0100?00122	10001??211
Asturi_jaack	121111?200	0010000000	-000000000	0000-100??	2000001222	2210110100
Sotocinctus	100?01??0a	0010000000	-000000000	0000-00000	2000001222	2100110200
Troch_bohe	1da111010b	a020000000	0222000222	0000-11011	2000012222	221111?210
Trochocys_parvu	1000?00000	0010000000	-002200220	0000-1????	2000012222	2210110210
Ludwig_trunc	101?????01	0010100000	-022222222	2000-12???	0000000122	00001-?210
Ctenocystis	011????000?	0?????0000	?000000000	?????????00	20?00?????	?????????000