

Stereom microstructure of columnal latera: a character for assessing phylogenetic relationships in articulate crinoids

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Abstract The stereom microstructure of columnal latera in various articulate crinoids is examined to ascertain its potential application in phylogenetic studies. Most show either a poorly ordered labyrinthic stereom or a more regularly ordered perforate stereom with lumina arranged in an en echelon pattern. Labyrinthic stereom is taxonomically widespread and is interpreted here as the plesiomorphic state. Perforate stereom, typically with an en echelon arrangement of elliptical lumina, appears confined to the Isocrinina and is considered to be apomorphic for that group. The absence of any development of perforate stereom in the bourgueticrinid *Democrinus* suggests that the bourgueticrinids have affinities with the comatulids rather than with the isocrinids. A second type of perforate stereom, with sinuous or straight lines of circular to elongate lumina, has been found only in *Pentacrinites* and may be autapomorphic for that group. The shape and spacing of stereom lumina on the columnal latera of different genera of isocrinids displays minor variation that may have some value for assessing phylogenetic affinity at genus and family level in taxa known only from columnals.

Keywords Crinoid · Articulata · Stereom · Phylogenetics

Introduction

Crinoids have been a common and diverse element of the marine biota since the Ordovician, and indeed during the Carboniferous and Permian appear to have exceeded the diversity of all other echinoderm taxa combined (Paul and Smith 1984). The complex multi-element skeleton of crinoids, like other echinoderms, confers upon them a wealth of morphological characters that have long formed the basis for their taxonomic classification (e.g. Miller 1821). With the almost universal acceptance of cladistics as a more objective method of analysing the significance of character distribution within living and fossil organisms, great steps have been made in the past three decades in revising the systematics and reinterpreting the phylogenies of many taxonomic groups, among them the Crinoidea. At higher taxonomic levels, cladistic analysis clearly is a powerful tool for establishing phylogenetic relationships although some degree of subjectivity inevitably arises from the identification and interpretation of morphological characters. In fossil organisms, where ontogenetic sequences are not available to check the development of a particular character, it may prove difficult to ascertain if a particular character in one high level taxon is actually homologous with a similar character in another. Among the Crinoidea interpretation of cup plating homology had remained virtually unchanged since the work of Miller (1821). Not until the mid-1990s did a reappraisal of these homologies allow a radical departure from previous phylogenetic models for the Class (Simms 1994). However, Simms' proposed homologies differ in part from those subsequently proposed by Ausich (1996) and, with the

Most of the photographs of Lower Jurassic taxa were taken at the Natural History Museum in London as part of my Ph.D. research between 1983 and 1986. These specimens are now held in the collections there but in some instances it has not been possible to identify precisely which specimen was used; these are indicated by BM without the full accession number. Other material is held in the Ulster Museum (BELUM) and Muschelkalkmuseum Ingelfingen.

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limited ontogenetic data available for the cup in extinct taxa, the issue remains open to debate.

Application of cladistic methodology to phylogenetic analysis within the Crinoidea is highly dependent on well-preserved specimens, those in which the state of numerous morphological characters can be assessed and compared with other taxa. Intact preservation of crinoids is notoriously subject to the vagaries of chance. After death, the multielement skeletons of crinoids disarticulate within days, or even hours, as the soft tissues connecting the ossicles decay (e.g. Donovan 1991). For most fossil crinoids intact preservation was a consequence of obrution (Seilacher et al. 1985)—the near instantaneous burial and death by an influx of sediment sufficient to exclude damage through subsequent scavenging or burrowing (Simms 1986). This necessarily excludes those taxa that inhabited environments less prone to such obrutational events. Indeed, many post-Palaeozoic crinoid species have been described on the basis only of dissociated remains, particularly columnals. These columnals may be distinctive and characteristic at particular stratigraphic levels, but incomplete knowledge of other aspects of the morphology of these species excludes many of them from cladistic analysis.

Cladistic methodology clearly is the best approach for inferring phylogenetic relationships at high taxonomic levels, but at lower taxonomic levels, such as species or genus, it is less useful. Taxonomic distinctions at these low levels commonly are based on relatively minor, qualitative and readily reversible, character changes such as the ornamentation, shape or number of elements, rather than on the clearly defined presence or absence of a specific character. At low taxonomic levels, a more pragmatic approach may be adopted for inferring phylogenetic relationships, based on the morphological similarity of those characters available coupled with stratigraphic proximity. In many cases, the evidence suggests that the fossil record for a particular group during a given time interval is much more complete than is generally assumed (Paul 1998), allowing evolutionary relationships to be inferred with some confidence (e.g. Howarth 1958; Simms 1989a). Where crinoid diversity was relatively low, as in the Hettangian to Pliensbachian (Lower Jurassic) of north-west Europe, a continuous stratigraphic series of morphologically similar taxa are more likely to represent an evolving lineage of species than a disjunct series of taxa that were unconnected by direct ancestor-descendent relationships. This certainly would appear to be the case for two groups of isocrinids, *Isocrinus* and *Balanocrinus*, from the Early Jurassic (Simms 1988a, 1989a). Of the eight species involved, three of *Isocrinus* and five of *Balanocrinus*, three are known almost exclusively from columnals and for one the crown is entirely unknown. However, based on pluricolumnals alone, stratigraphically successive taxa are similar but can

be distinguished on morphometry and/or columnal shape and ornamentation. Both lineages show distinct trends in certain characters, which have been interpreted as heterochronous in origin (Simms 1990).

Although there is considerable justification for regarding the members of each of these two parallel lineages as having ancestor-descendent relationships, the relationship between the lineages is more conjectural. Simms (1985, 1988a) argued that *Balanocrinus* was a neotenuous offshoot from the *Isocrinus* lineage. This was based on the morphological similarities between the stems of immature *Isocrinus psilonoti* and mature *Balanocrinus quiaiosensis*, which he considered to be the earliest species of *Balanocrinus*. However, columnal morphospecies nominally assigned to *Balanocrinus* do occur both earlier, such as '*Balanocrinus antiquus*' Loriol, from the Hettangian, and later, for instance *Balanocrinus subteres* (Münster), from the Upper Jurassic. Both Roux (1981) and Klikushin (1982) recognised the Balanocrininae as a subfamily of the Isocrinidae to which they assigned *Balanocrinus* and several other genera. They considered this clade to have diverged from other isocrinids in the Triassic and persisted to at least the early Neogene. Specifically, Klikushin (1979b, 1982) linked the origins of the Balanocrininae to *Laevigatocrinus*, an Early Carnian (Upper Triassic) genus to which he assigned several species. However, Hagdorn (this volume) restricts this genus to just the highly distinctive type species, *Laevigatocrinus laevigatus*, assigning other species to *Balanocrinus* s.l. or to *Eckicrinus*.

Among isocrinids, homeomorphy probably is very common. Only a limited range of basic columnal morphologies is possible, e.g., circular, pentagonal, stellate, so that broad similarities of columnal shape alone cannot be considered a sound basis for considering close phylogenetic relationship between species. The Late Triassic '*Balanocrinus*' *subcrenatus* is known only from columnals, with nothing known of the crown, and is separated from any broadly similar younger columnals (e.g. Loriol's '*Balanocrinus*' *antiquus*) or the better documented Early Jurassic species of *Balanocrinus* (Simms 1989a) by more than 20 million years. This considerable time gap does not preclude a direct phylogenetic relationship between these taxa but, with so little known about their morphology, it might appear difficult to establish whether or not there is a close phylogenetic link between them. Are these older and/or younger taxa actually representatives of the well-documented Sinemurian–Pliensbachian lineage or are they homeomorphs that arose from an isocrinid ancestor independently of the Sinemurian–Pliensbachian *Balanocrinus* lineage in question. How might this question be resolved in the face of the very limited morphological data available for some of these nominal taxa? What is needed is some character that can be recognised even in isolated

columnals, a character that is inherent to all of them, and that reflects phylogenetic relationships more closely than functional or ecophenotypic constraints.

Stereom microstructure of columnals: background to the research

One of the fundamental characters that defines the Phylum Echinodermata is the possession of a multi-element endoskeleton composed of high-magnesium calcite ossicles with a stereom microstructure, an orderly or labyrinthine network of cavities permeated with soft tissue termed stroma. Each ossicle is formed of an optically continuous crystal of calcite, a readily cleaved mineral, with the stereom/stroma composite imparting a much greater strength to what is an inherently brittle material. Additional advantages to the organism conferred by this stereom structure include a reduction in energy required for the biomineralisation process; a skeletal density significantly lower than if the ossicles were solid calcite; and the provision of a vast range of attachment points for soft tissues.

Variation in stereom morphology has been recognised for more than a century and a half (see Smith 1980 for early references) but it is only since the 1970s that any detailed investigation has been undertaken of this variation and its possible significance. Crinoids figured prominently in some of these early investigations, with papers by Edward Gluchowski, Vladimir Klikushin, Brad Macurda, Dave Meyer and Michel Roux (Gluchowski 1982; Klikushin 1979a; Macurda and Meyer 1975; Macurda et al. 1978; Macurda and Roux 1981; Roux 1970, 1975, 1977, 1981). Echinoids are the other extant echinoderm class in which the stereom microstructure has been investigated in detail, with the substantial work of Andrew Smith being particularly important here (Smith 1980). Interest in this field might seem to have waned subsequently but in fact aspects of what was learned in the 1970s and 1980s are now routinely applied to the interpretation of extinct echinoderms (e.g. Clausen and Smith 2005, 2008).

The biometric studies undertaken by Roux (Roux 1970, 1975; Macurda and Roux 1981) focused on aspects of the growth of the stereom, particularly on the articula of crinoid columnals, and its potential implications in terms of function and taxonomy. Other papers (e.g. Macurda and Meyer 1975; Macurda and Roux 1981) looked more widely at other parts of the crinoid endoskeleton, such as cirri, brachials and cup plates. Smith's work (Smith 1980) was particularly significant in identifying the relationship between stereom morphology and associated tissues and, although based on echinoids, has relevance across the entire Class. All of these papers focused largely on articulation or attachment surfaces and accordingly stressed the

functional aspects of the stereom being examined. As such, the stereom morphology they described is more likely to reflect function than phylogeny.

Consideration of crinoid columnals suggests that although the morphology of articulating surfaces may be strongly influenced by mechanical constraints, this is less likely to be the case for columnal latera. Columnal latera among isocrinids may be variously ornamented with small tubercles or ridges but in the majority of taxa the latera are smooth at the macroscopic scale. Although enveloped by a thin tissue layer, the columnal outer surface does not serve for the attachment of motile tissue and hence is not subject to the more obvious functional constraints imposed on articula. Clearly the latera are not entirely 'functionless', as they represent an interface between the exterior and interior of the columnal and must maintain the structural integrity of the columnal as a whole. However, such constraints are mechanically less demanding than those imposed on articula and hence characteristics of the stereom microstructure might more clearly reflect underlying phylogenetic factors. Despite the plethora of papers dealing with functional and ontogenetic aspects of crinoid articular stereom, the possible phylogenetic significance of any similarities or differences in the stereom of crinoid latera has not previously been addressed other than very briefly by Gluchowski (1982) and by Simms (1985, 1988a, 1989a). From a limited survey of taxa undertaken in conjunction with wider research on Lower Jurassic crinoids, Simms (1985, 1988a) suggested that the pattern of lumina in the stereom of columnal latera was significant at the family level and indicated a close phylogenetic relationship between Early Jurassic *Isocrinus* and *Balanocrinus*. The current study is intended to pursue this investigation further and to assess at what taxonomic level this particular character might be useful. Can it be used as a tool to establish the degree of phylogenetic relationship between morphologically similar columnals at widely separate stratigraphic levels or does it reflect relationships at only very high taxonomic levels and therefore has only limited utility? Ideally such a study would examine the microstructure of a large sample of crinoid taxa, both fossil and extant but, in this instance, I have been constrained both by availability of material and by access to a scanning electron microscope (SEM). The high level taxonomy of the crinoids referred to in this account follows that of Simms et al. (1993).

Materials and methods

A range of fossil and recent articulate crinoid material has been examined for this study. The fossil columnals examined were from various stratigraphic levels, in the

Carnian to Rhaetian stages of the Triassic and the Hettangian to Toarcian stages of the Jurassic, and they encompass various taxa within the families Encrinidae and Pentacrinitidae, the Suborder Isocrinina, and the Order Millericrinida. Three extant articulate crinoids were also examined; two species of the isocrinid *Endoxocrinus* and one of the bourgueticrinid *Democrinus*. All of the specimens were examined at relatively low power ($< \times 400$) using SEM facilities at the Natural History Museum, London, and Queen's University Belfast.

The recent material, of *Endoxocrinus* and *Democrinus*, is very well preserved and provides an invaluable comparison against which to judge fossil preservation. Preservation can be a major limitation to any study of the columnal microstructure in fossil material. On a macro scale, preservation can appear very good, but syntaxial overgrowth of the microstructure can partly or completely fill stereom pore space. This is more likely to occur in carbonate-rich successions rather than in mudstone sequences, as observed by Klikushin (1979a) and Gluchowski (1982), and would appear to be the case for the samples of *Encrinus liliiformis* that were examined. The columnal latera of these showed a fairly smooth surface lacking any distinct lumina. Columnals may also experience post-burial etching which can remove the surface of the latera to an unknown depth and preferentially etch cleavage planes near the surface. This clearly has occurred in the samples of *Holocrinus dubius* (Fig. 3c, d) and even more so in the columnals of *Isocrinus* sp. from Kardolina (Fig. 3e, f). Lumina are developed on the latera of these etched columnals but it is unclear to what extent these reflect the original surface configuration of the latera or might be an artifact of etching. Relatively minor etching is apparent in the specimen of *Isocrinus psilonoti* (Fig. 2d) while other specimens, such as *Isocrinus robustus* (Fig. 2e) and *Balanocrinus subteroides* (Fig. 2b), appear little modified by comparison with the Recent *Endoxocrinus* (Fig. 2a, b). Twenty-six samples were examined from different stratigraphic levels and/or localities, with each sample comprising between one and three specimens. Seven of these proved too poorly preserved, either through excessive etching or syntaxial overgrowth, to be informative.

Observations

Andrew Smith (1980), in his seminal work on echinoderm microstructure, defined ten types of stereom fabric on the basis of its three dimensional configuration of pores and trabeculae. About half of these occur widely in different parts of the crinoid endoskeleton but within the relatively small sample size available for this study just two types of

Fig. 1 All figures are of columnal latera unless otherwise indicated. Scale bar 100 μm . **a** En echelon perforate stereom with elliptical lumina. *Balanocrinus quiaiosensis* de Loriol. Jurassic, Sinemurian, Charmouth Mudstone Formation, Quedgeley, Gloucestershire, England. BM. **b** En echelon perforate stereom with elliptical lumina. *Balanocrinus subteroides* (Quenstedt). Jurassic, Pliensbachian, Charmouth Mudstone Formation, Blockley, Gloucestershire, England. BM E70552. **c** En echelon perforate stereom with weakly elliptical lumina. *'Isocrinus' angulatus* (Oppel). Jurassic, Hettangian, Waterloo Mudstone Formation, Larne, Co. Antrim, Northern Ireland. BELUM K2010.4. **d** En echelon perforate stereom with elliptical lumina, slightly etched. *Isocrinus psilonoti* (Quenstedt). Jurassic, Hettangian, Blue Lias Formation, Tewkesbury, Gloucestershire, England. BM. **e** En echelon perforate stereom with elliptical lumina. *Isocrinus robustus* (Wright). Jurassic, Pliensbachian, Charmouth Mudstone Formation, Scunthorpe, Humberside, England. BM. **f** En echelon perforate stereom with near circular lumina. *Hispidocrinus scalaris* (Goldfuss). Jurassic, Sinemurian, Charmouth Mudstone Formation, Bishops Cleeve, Gloucestershire, England. BM. **g** En echelon perforate stereom with elliptical lumina. *Hispidocrinus schlumbergeri* (de Loriol). Jurassic, Sinemurian, Charmouth Mudstone Formation, Charmouth, Dorset, England. BM. **h** Sinuous perforate stereom with circular to elliptical lumina. *Pentacrinites fossilis* Blumenbach. Jurassic, Sinemurian, Charmouth Mudstone Formation, Charmouth, Dorset, England. BM

stereom, labyrinthic (e.g. Fig. 2d) and perforate (e.g. Fig. 1e), were recognised on columnal latera. These can be described as follows, based on the descriptions of Smith (1980) and observations made during this study:

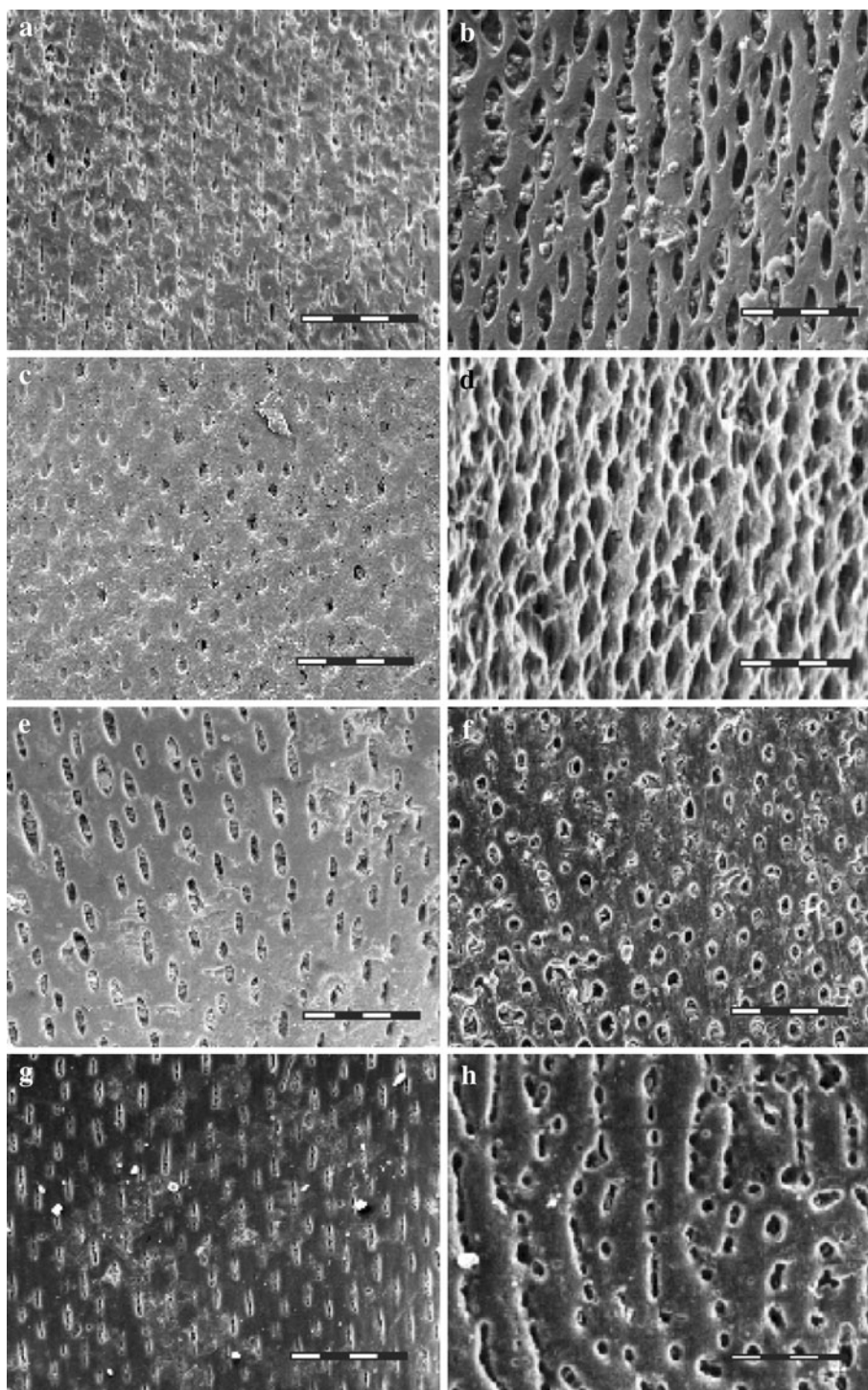
Labyrinthic stereom

This forms a completely unorganised three-dimensional tangle of trabeculae which may range from a coarse open structure to a finer, more compact, arrangement. The shape and arrangement of pores is difficult to define as this type of stereom never forms a planar surface.

Perforate stereom

Smith (1980) described this as forming layers usually thicker than the maximum diameter of the small circular pores which penetrate it. He distinguished simple from irregular perforate stereom on the basis of its cross-sectional structure, but such a division cannot be applied in this study which has examined only the surface configuration of the stereom. Perforate stereom of crinoid columnal latera encountered during this study commonly differs from that described by Smith (1980) in having markedly elliptical pores arranged in an en echelon pattern, a configuration termed here 'en echelon perforate stereom'.

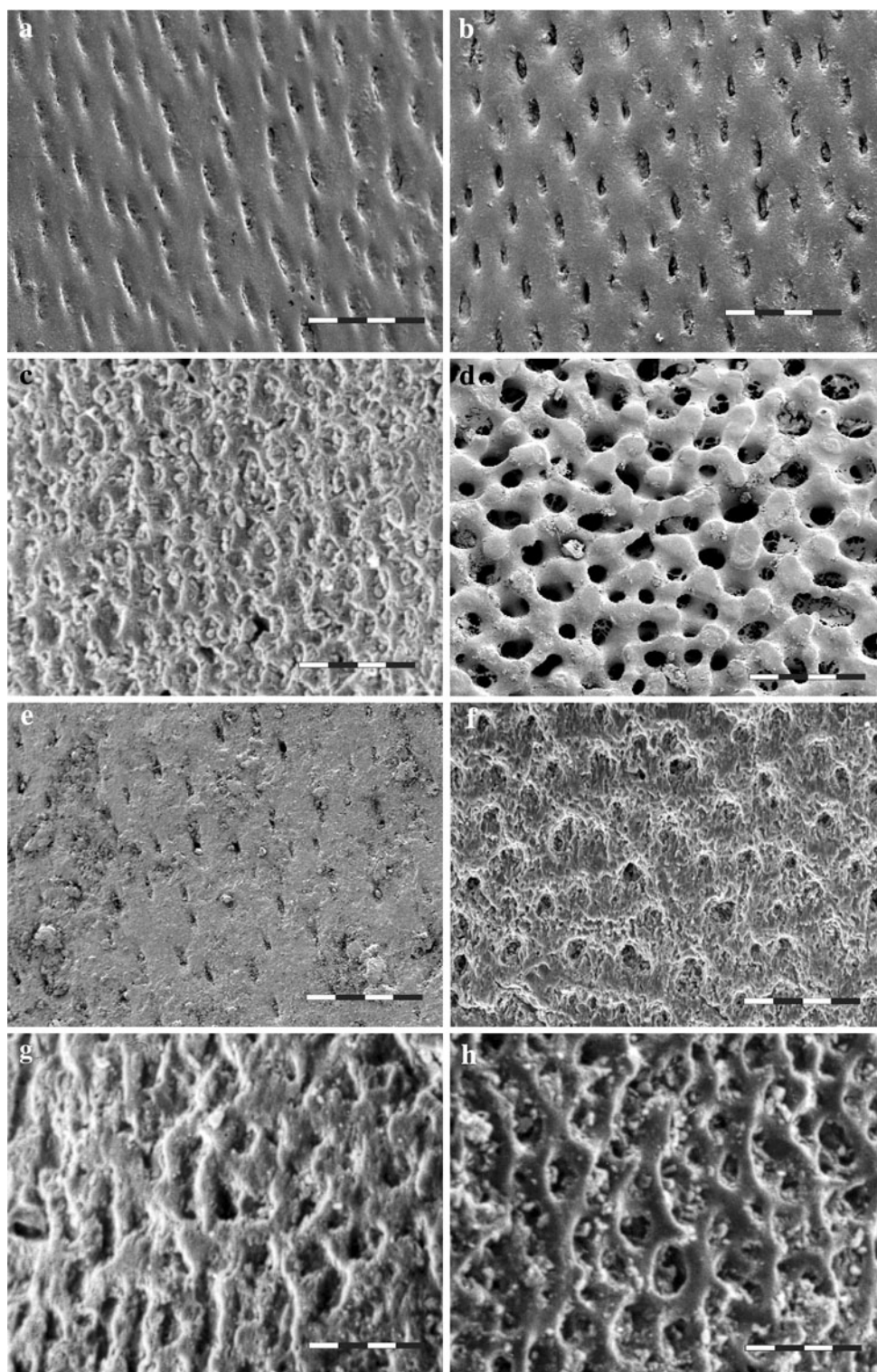
There is some variation in the shape and configuration of stereom lumina across the latera of individual columnals (Fig. 3a) but this appears relatively minor compared with the differences that are seen between different taxa. Perforate stereom appears confined to representatives of the Isocrinina and exhibits a modest range of patterns of



stereom lumina on the columnal latera (Figs. 1a–g, 2a, b, e, f). The most commonly encountered arrangement consists of an en echelon pattern of elliptical to lanceolate lumina. Lumina typically are c.10–20 μm wide, with the more elongate ones up to c.40 μm long. This pattern is seen in both species of *Endoxocrinus* (Fig. 2a, b), the extant isocrinid genus examined, where lumina account for about

15–20% of the lateral surface and are separated by areas of smooth unperforated calcite. Among some of the Early Jurassic isocrinids the lumina account for a much greater proportion of the surface, perhaps 35–40% in the case of *Balanocrinus subteroides* (Fig. 1b) or *Isocrinus psilonoti* (Fig. 1d). An intermediate pattern of en echelon elliptical or lanceolate lumina is seen also in some of the other Early

Fig. 2 All figures are of columnal latera unless otherwise indicated. *Scale bar* 100 μ m. **a** En echelon perforate stereom with elliptical lumina. *Endoxocrinus parrae* (Gervais). Recent. BELUM K2010.1.2. **b** En echelon perforate stereom with elliptical lumina. *Endoxocrinus prionodes* H.L. Clark. Recent BELUM K2010.2.2. **c** ?Labyrinthic stereom. *Chariocrinus wuerttembergicus* (Oppel). Jurassic, Toarcian, Whitby Mudstone Formation, Cleeve Hill, Gloucestershire, England. BM E70412. **d** Labyrinthic stereom. *Democrinus* cf. *brevis*. Recent. BELUM K2010.3.2. **e** En echelon perforate stereom with very small, widely spaced elliptical lumina. *Laevigatocrinus laevigatus* (Münster). Triassic, Carnian, Cassian Formation, Cion del Coute, Italy. Muschelkalkmuseum Ingelfingen. **f** En echelon perforate stereom with weakly elliptical lumina. '*Balanocrinus*' *subcrenatus* (Münster). Triassic, Carnian, Cassian Formation, St Cassian, Italy. BMNH E67484 g. Labyrinthic stereom. *Plicatocrinus inornatus* Simms. Jurassic, Toarcian, Beacon Limestone Formation, Watton Cliff, Dorset, England. BM E70612. **h** Labyrinthic stereom. *Millerocrinus* ? *alpinus* (Gümbel). Jurassic, Toarcian, Marlstone Rock Formation, Thorncombe Beacon, Dorset, England. BM E70515

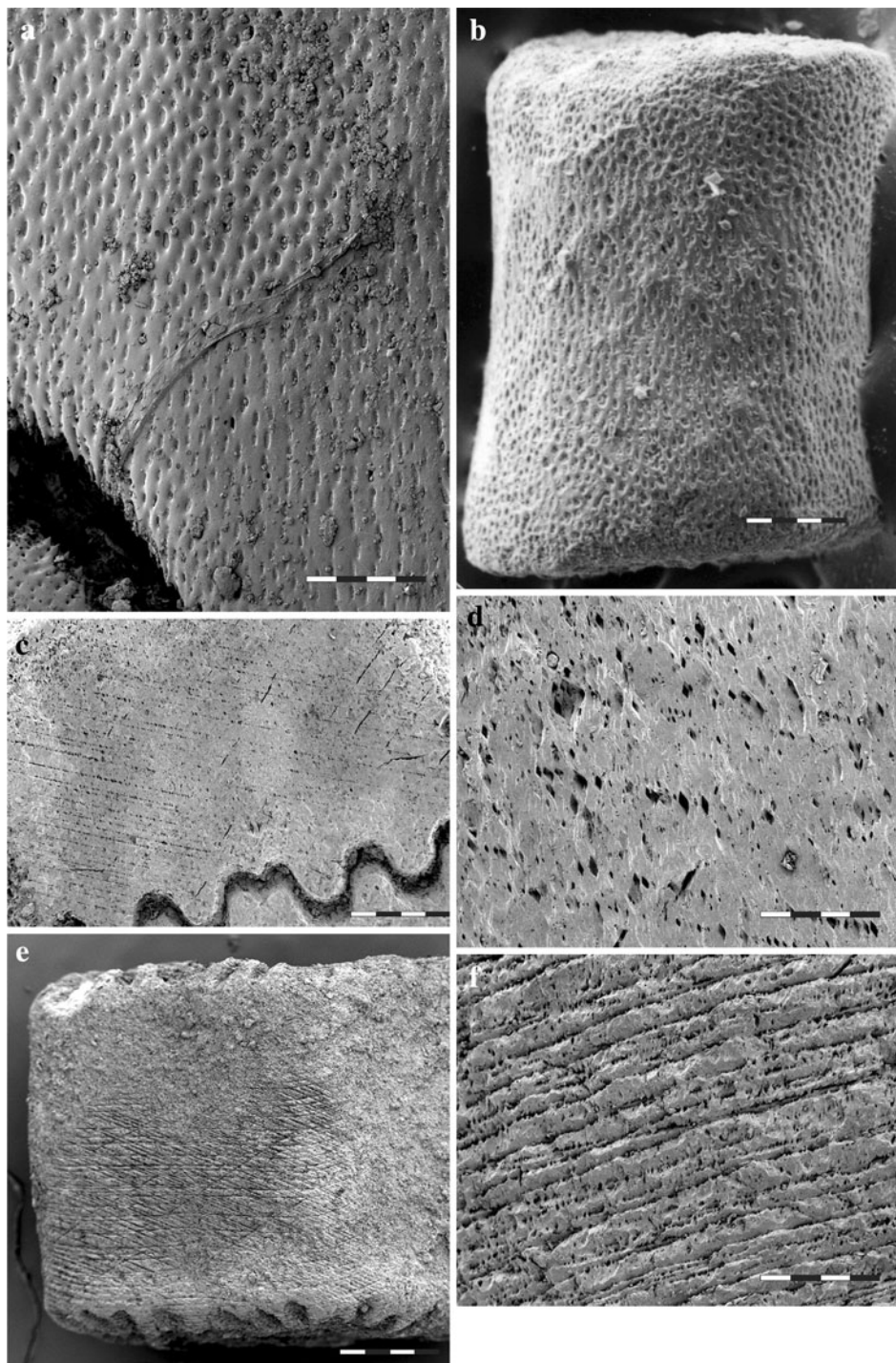


Jurassic isocrinids; *Isocrinus robustus* (Fig. 1e), *Balanocrinus quaiiaosensis* (Fig. 1a) and *Hispidocrinus schlumbergeri* (Fig. 1f). Two other Early Jurassic species, '*Isocrinus*' *angulatus* (Fig. 1c) and *Hispidocrinus scalaris* (Fig. 1g), show a pattern of very weakly elliptical or near circular lumina that is more typical of the perforate

stereom described by Smith (1980). These too are arranged en echelon on a smooth surface but cover only about 15% of the surface. Columnals of the Late Triassic '*Balanocrinus*' *subcrenatus* (Fig. 2f) are rather poorly preserved but appear to show a similar arrangement and coverage. En echelon lumina are also seen in the late Triassic

Fig. 3 Scale bar 100 μm unless indicated otherwise

a *Endoxocrinus parvae* (Gervais). Recent. Detail of nodal columnal adjacent to cirral scar, showing minor variation in configuration of en echelon perforate stereom structure. BELUM K2010.1.2.
b *Balanocrinus subteroides* (Quenstedt). Jurassic, Pliensbachian, Charmouth Mudstone Formation, Blockley, Gloucestershire, England. Columnal of pentacrinoid larva, with synarthrial articularia, showing both labyrinthic and en echelon perforate stereom. BM E70553. Scale bar 150 μm .
c Etched cleavage planes on columnal latus of *Holocrinus dubius* (Goldfuss). Triassic, Anisian, Jena Formation, Oberer Wellenkalk, Rittersdorf, Thuringia, Germany. Muschelkalkmuseum Ingelfingen. Scale bar 400 μm .
d Etched cleavage planes on columnal latus of *Holocrinus dubius* (Goldfuss) showing development along them of lumina (?preservational artifacts). Triassic, Anisian, Jena Formation, Oberer Wellenkalk, Rittersdorf, Thuringia, Germany. Muschelkalkmuseum Ingelfingen.
e Etched cleavage planes on columnal latus of '*Isocrinus*' sp. Triassic, Rhaetian, Fatra Formation, Tatra Mountains, Slovakia. BELUM K2010.5.2. (from Peter Ledvák Collection). Scale bar 400 μm .
f Etched cleavage planes on columnal latus of '*Isocrinus*' sp. Triassic, Rhaetian, Fatra Formation, Tatra Mountains, Slovakia. BELUM K2010.5.2. (from Peter Ledvák Collection)



Laevigatocrinus laevigatus (Fig. 2e) but in this species, the lumina account for considerably less than 10% of the surface area, a figure significantly lower than in the other isocrinids examined.

Two of the taxa examined, the Mid-Triassic *Holocrinus dubius* (Fig. 3c, d) and the Late Triassic *Isocrinus* sp. from Kardolina (Fig. 3e, f), are significantly etched but, nonetheless, show an apparent arrangement of lumina on the

latera that closely resembles that seen in the well-preserved isocrinid material already described. In both of these taxa, the lanceolate lumina on these etched surfaces are significantly smaller than in other taxa examined, with those in *Isocrinus* sp. (Kardolina) being especially tiny at barely 5 μm across. These lumina are arranged en echelon along etched cleavage planes that cut through the columnals at a low angle (c.30° from horizontal). The main distinction

between these and the en echelon patterns on the other columnals described is their relatively low angle compared with the much more steeply en echelon patterns (c.75–80° from horizontal) seen on the other columnals. This, together with their anomalously small size, suggests that they may be preservational artifacts rather than primary features.

Of the other taxa examined most have what appears to be a rather random stereom arrangement that conforms with Smith's (1980) description of labyrinthic stereom. These taxa include the extant bourgueticrinid *Democrinus brevis* (Fig. 2d), the Early Jurassic millericrinids (s.l.) *Millericrinus ? alpinus* (Fig. 2h) and *Plicatocrinus inornatus* (Fig. 2g), and the Early Jurassic isocrinid *Chariocrinus wuerttembergicus* (Fig. 2c). The surfaces between lumina on these columnals are generally irregular and not smooth as in the isocrinids described earlier, an observation consistent with Smith's statement that this type of stereom never forms a planar surface.

The final stereom arrangement has, so far, been observed only in the Early Jurassic *Pentacrinites fossilis*, representative of a clade considered to have a sister group relationship to the comatulids s.l. In *Pentacrinites*, the latera appear to be formed of perforate stereom in which lumina are circular to highly elongate ellipses, in some cases >50 µm long, arranged in straight to gently sinuous discontinuous rows separated by gently convex raised areas (Fig. 1h).

Interpretation

Function and development of lateral stereom

The latera of crinoid columnals represents an interface between the animal and its external environment. A thin layer of tissue separates the solid material of the columnal from the environment and hence the lumina seen on the latera probably serve as points of connection between the external tissue and the internal stroma. For this reason alone it seems likely that most, if not all, crinoid columnals will have abundant lumina on the latera and that their absence in fossil material is an artifact of preservation. The proportion of pore space for a given area of latera may also be influenced by this requirement of connectivity between the interior and the exterior of the columnal.

In non-isocrinid crinoids, and the isocrinid *Chariocrinus*, the columnal latera are constructed of labyrinthic stereom. Smith (1980) found labyrinthic stereom to occur very widely and to be associated with all types of tissue. He also noted that commonly it was associated with moderate to fast stereom growth and that a reduction in growth rate could lead to the development of perforate stereom.

Perforate stereom, in which the circular to elliptical lumina are arranged in a moderately to steeply en echelon configuration, is found among most of the isocrinids with the apparent exception in this sample of the Early Jurassic *Chariocrinus*. Smith (1980) described perforate stereom as forming during periods of slow stereom growth, with denser inner and outer layers providing resistance to bending stresses and protection against abrasion. The presence of small en echelon lumina aligned along low angle cleavage planes on the latera of etched columnals of *Holocrinus dubius* and of *Isocrinus* sp. from Kardolina suggests that the en echelon configuration seen in well-preserved columnals might perhaps reflect underlying cleavage planes. However, the significantly smaller size and spacing of the lumina on the etched columnals (<10 µm across), compared with those on well-preserved columnals (typically >15 µm), suggests that those on the etched columnals are a preservational artifact. Further work would be needed to ascertain if the configuration of stereom lumina on isocrinid columnal latera actually reflects any underlying structural control.

Phylogenetic aspects

Smith (1980) noted that some stereom arrays were restricted to particular echinoid orders, implying phylogenetic as well as ontogenetic and functional controls. Gluchowski (1982) also suggested that certain types of lateral stereom with large pores might have some phylogenetic significance. The present study indicates that the stereom of columnal latera is indeed significant for crude discrimination at high taxonomic levels, but might it also be used as a discriminant at lower levels?

Species-level discrimination

The two extant species of *Endoxocrinus* examined might be expected to show very closely similar lateral stereom, particularly considering suggestions that *Endoxocrinus parrae* and *E. prionodes* may even be conspecific (Meyer et al. 1978; Oji 1990). Both have the typical en echelon perforate stereom seen widely in isocrinids, but they are certainly not identical. In *Endoxocrinus parrae*, there is a noticeably sharper demarcation between the stereom lumina and the intervening planar areas than is seen in *E. prionodes*, where instead the transition from the edges of the lumina to the intervening planar surface is significantly more rounded (Fig. 2a, b). Oji (1990) suggested that the macroscopic differences between these two species reflected ecophenotypic variation linked to habitat depth. The stereom differences may also perhaps be a consequence of these habitat differences but alternatively it may indicate that the two are in fact separate species after all.

Genus and family level discrimination in Early Jurassic isocrinids

Among Early Jurassic isocrinids encountered in north-west Europe several discrete genera, *Isocrinus*, *Balanocrinus*, *Hispidocrinus* and *Chariocrinus*, can be recognised (Simms 1988a, 1989a). Stratigraphic and morphologic criteria indicate ancestor–descendant relationships between three species of *Isocrinus* spanning the Hettangian to Pliensbachian stages; *I. psilonoti*, *I. tuberculatus* and *I. robustus*. Several other species were assigned to the genus, although with less certainty about their relationship to this ‘central’ lineage. A second lineage, assigned to *Balanocrinus*, shows similar strong evidence for ancestor–descendant relationships between four species spanning the Sinemurian–Pliensbachian stages; *Balanocrinus quiaiosensis*, *B. subteroides*, *B. gracilis* and *B. solenotis*. It had been suggested that the *Balanocrinus* lineage could be traced back into the Late Triassic (Klikushin 1979b, 1982), but Simms (1985, 1988a) suggested, on morphological grounds, that it arose as a neotenous offshoot from the ‘central’ *Isocrinus* lineage. In support of this, there is a close similarity between the lateral stereom of the Early Jurassic *Isocrinus* and *Balanocrinus* (Fig. 1b, d). This is distinct from the configuration seen in the Late Triassic (Carnian) ‘*Balanocrinus*’ *subcrenatus*, where the lumina are almost circular and widely spaced (Figs. 2f, 4).

Two other Early Jurassic species are assigned to a third genus, *Hispidocrinus*, on account of their distinctive morphology, with markedly stellate columnals bearing relatively small cirral scars and with relatively short noditaxes (<8 columnals) compared with *Isocrinus* (>12 columnals). The relationship of this genus to other isocrinids in the Early Jurassic or Late Triassic is unclear. In the type species, *Hispidocrinus scalaris*, the stereom on columnal latera is of classic perforate type, with near circular lumina (Fig. 1f) arranged en echelon and separated by planar intervening areas. This arrangement is different from Early Jurassic *Isocrinus* and *Balanocrinus* in which the lumina are markedly elliptical (Fig. 1a, b, d, e). However, its putative Early Jurassic descendant, *Hispidocrinus schlumbergeri* (Fig. 1g), has lateral stereom that more closely resembles these genera (Fig. 4), perhaps indicating a reversion back to the pattern seen in the central *Isocrinus* lineage.

Another isocrinid has recently been recognised as a distinct species in the latest Triassic (Rhaetian) and earliest Jurassic (Hettangian) in north-west Europe. This was figured in the 19th Century (Loriot 1884–89) as *Isocrinus angulatus*, although the original name was a nomen nudum (Oppel 1856–58). It was dismissed by Simms (1989a) as a synonym of *Isocrinus psilonoti* but abundant new material, albeit disarticulated, from the basal Hettangian Stage has

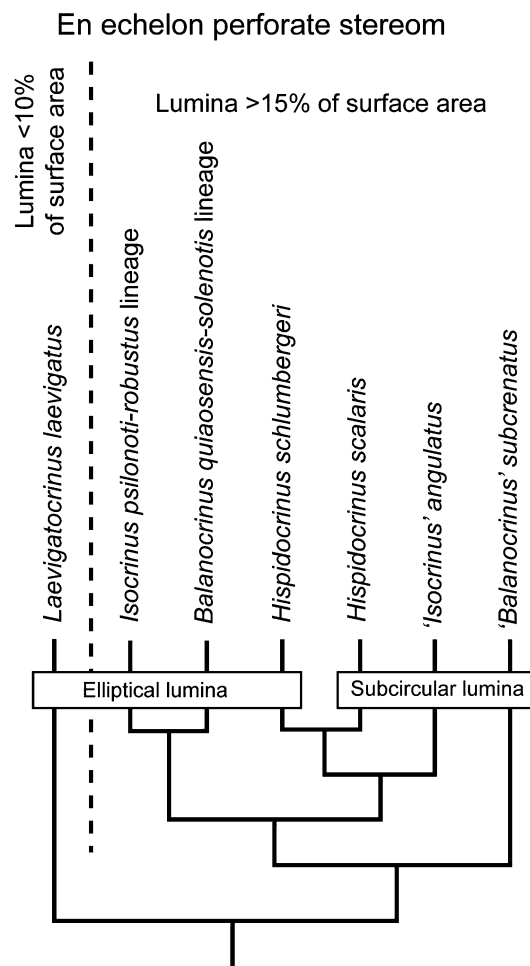


Fig. 4 Cladogram showing relationship between various Late Triassic and Early Jurassic crinoid species and species groups, as inferred from the shape and area of stereom lumina on columnal latera

revealed that these two taxa are not conspecific. *Isocrinus angulatus* never attains the large size of *I. psilonoti*, has consistently shorter noditaxes (<9 columnals) and a more markedly stellate columnal outline. In this respect, it is not dissimilar to *Hispidocrinus scalaris* and *H. schlumbergeri* and, intriguingly, the shape and configuration of stereom lumina on columnal latera (Fig. 1c) is more reminiscent of *H. scalaris* (Fig. 1f) than of other Early Jurassic isocrinids. Morphometric analysis of this species has yet to be undertaken but this observation suggests that its affinities may perhaps lie with *Hispidocrinus* (Fig. 4).

Of the Early Jurassic isocrinids examined for this study, one stands out as being anomalous. This is *Chariocrinus wuerttembergicus*, a small isocrinid that is common in the British Toarcian. Unlike all of the other isocrinids examined, which have perforate stereom on columnal latera, this species appears to have lateral stereom with a structure more akin to unordered labyrinthic stereom (Fig. 2c).

High-level discrimination

The distinction, based on the lateral stereom, between most of the isocrinids examined and the non-isocrinids has already been alluded to, with most of the former possessing perforate stereom and the latter labyrinthine stereom. However, other macroscopic characters can generally be used to identify phylogenetic affinities at this high level without relying on this character alone. Labyrinthine stereom has been identified on the columnal latera of representatives of four high level taxa; in *Millericrinus ? alpinus* (Millericrinina), *Plicatocrinus inornatus* (Cyrtocrinina), *Democrinus brevis* (Bourgueticrinidae) and the seemingly anomalous case of *Chariocrinus wuerttembergicus* (Isocrinina). The precise phylogenetic relationship between the millericrinids and cyrtocrinids is unclear as many of their apparent similarities are actually plesiomorphic characters and hence uninformative, but they are treated together here as Millericrinida.

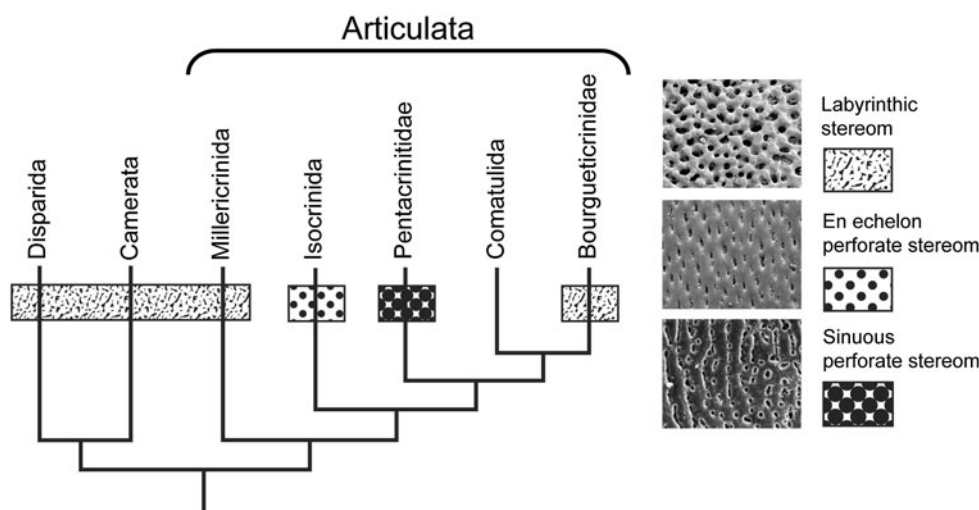
The occurrence of labyrinthine stereom on the columnal latera of representatives of three or four discrete taxonomic groups suggests that this is the plesiomorphic condition, and that the perforate stereom, with en echelon lumina, seen in most of the isocrinids examined, is apomorphic and arose after the isocrinid and ‘non-isocrinid’ clades had diverged (Fig. 5). Gluchowski (1982) reported labyrinthine stereom on the columnal latera of some Palaeozoic crinoids (disparids and monobathrid camerates) which, coupled with its taxonomically widespread occurrence in other crinoid taxa, also suggests that this is the plesiomorphic state for columnal latera microstructure.

Bourgueticrinids have in the past been assigned to the Millericrinida (Roux 1977; Pisera and Dzik 1979) but others have considered them as neotenous derivatives of either a comatulid or isocrinid stock (Rasmussen 1978; Simms 1988b; Simms et al. 1993). The presence of labyrinthine

stereom on the latera of *Democrinus* columnals, although a plesiomorphic trait, is nonetheless significant for resolving this issue. Both comatulids and isocrinids pass through a ‘pentacrinoïd’ larval stage in which they possess a tiny (<1 mm diameter) stem with bifascial synarthrial articularia and hence, on the grounds of columnal morphology alone, the bourgueticrinids could have evolved from either group (Simms 1988b). In comatulids, the stem is lost as the centrodorsal develops while in isocrinids continued growth of the stem leads to the development of typical symplectial articularia (Simms 1989b). Examination of pentacrinoïd larval columnals of *Balanocrinus subteroides* (Fig. 3b) shows that even at this small size they have developed the en echelon pattern of perforate stereom typical of most isocrinids. This contrasts markedly with the latera of *Democrinus* columnals, which is entirely labyrinthine (Fig. 2d). The absence of an echelon perforate stereom on *Democrinus* columnals suggests that bourgueticrinids more probably are neotenous derivatives of the comatulids rather than isocrinids (Fig. 5), retaining the stem which ordinarily would be lost in adult comatulids.

The lateral stereom of the Early Jurassic *Pentacrinites fossilis* (Fig. 1h) appears distinct both from the regular perforate stereom of isocrinids and the more chaotic labyrinthine stereom of millericrinids, cyrtocrinids and bourgueticrinids. It might perhaps be interpreted as somewhere in between these two. The surface, although having gently convex ridges between rows of lumina, is much more planar than in typical labyrinthine stereom yet the configuration of the lumina is much more irregular than in the perforate stereom of isocrinids and, in that respect, resembles labyrinthine stereom. It is suggested here that this ‘sinuous perforate stereom’ in *Pentacrinites* arose independently from the apomorphic state represented by labyrinthine stereom (Fig. 5). Although some authors (Roux

Fig. 5 Cladogram showing relationships between major crinoid taxa as inferred from columnal latera stereom structure



1981) have suggested a close phylogenetic relationship between *Pentacrinites* and other isocrinids, the more widely held view is that the pentacrinids are sister group to the comatulids s.l. (Rasmussen 1978; Simms 1988b; Simms et al. 1993). If this were the case then the distinctive arrangement of lateral stereom in *Pentacrinites* is an autapomorphy for that clade rather than a variation of the en echelon perforate stereom seen widely in the isocrinids.

Conclusions

Examination of the microstructure of columnal latera in a variety of fossil and extant crinoid taxa has found that most can be grouped into one or other of two main stereom types. Most isocrinids have perforate stereom in which stereom lumina, typically elliptical, are arranged in an en echelon pattern. Most non-isocrinids examined, which includes millericrinids, cyrtocrinids and bourgueticrinids, have columnal latera composed of poorly ordered labyrinthic stereom. Labyrinthic stereom is interpreted as the plesiomorphic state for columnal latera, with en echelon perforate stereom as an apomorphy of the Isocrinina. A third stereom pattern, so far seen only in the Early Jurassic *Pentacrinites*, has straight to sinuous rows of lumina and appears to show aspects of both labyrinthic and perforate stereom. It is interpreted here to have arisen independently of the perforate stereom seen in the Isocrinina and, pending examination of other representatives, is considered to be an autapomorphy of the Pentacrinidae.

Variations in shape and spacing of the stereom lumina in isocrinids may be significant for genus or family level discrimination within the Isocrinina and may prove of value in resolving phylogenetic relationships in poorly known taxa.

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