Chapter 13

Cambrian echinoderm diversity and palaeobiogeography

SAMUEL ZAMORA1*, BERTRAND LEFEBVRE2, J. JAVIER ÁLVARO3, SÉBASTIEN CLAUSEN4, OLAF ELLICKI5, OLDRICH FATKA6, PETER JELL7, ARTEM KOUCHINSKY8, JIH-PAI LIN9, ELISE NARDIN10, RONALD PARSLEY11, SERGEI ROZHNOV12, JAMES SPRINKLE13, COLIN D. SUMRALL14, DANIEL VIZCAINO15 & ANDREW B. SMITH1

1Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK
2UMR CNRS 5276, Université Lyon 1 & ENS-Lyon, 69622 Villeurbanne, France
3Centro de Astrobiología (CSIC/INTA), Ctra. de Torrejón a Aljalvir km 4, 28850 Torrejón de Ardoz, Spain
4Géosystèmes, UMR 8157 and 7207 CNRS, Université des Sciences et Technologies de Lille, 59655 Villeneuve d’Ascq, France
5Geological Institute, Freiberg University, Bernhard-von-Cotta Street 2, 09599 Freiberg, Germany
6Department of Geology and Palaeontology, Faculty of Science, Charles University, Albertov 6, Praha 2, 128 43 Czech Republic
7Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia
8Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden
9Geological Institute, Freiberg University, Bernhard-von-Cotta Street 2, 09599 Freiberg, Germany
10State Key Laboratory of Paleobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China
11Department of Earth and Environmental Sciences, Tulane University, New Orleans, LA 70118, USA
12Paleontological Institute RAS, Profsoyuznaya St 123, 117997 Moscow, Russia
13Department of Geosciences, Jackson School of Geosciences, University of Texas, Austin, TX 78712-0254, USA
14Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996, USA
157 rue J.-B. Chardin, Maquens, 11090 Carcassonne, France
*Corresponding author (e-mail: samuel@unizar.es)

Abstract: The distribution of all known Cambrian echinoderm taxa, encompassing both articulated specimens and taxonomically diagnostic isolated ossicles, is documented for the first time. The database described by 2011 comprises 188 species recorded from 65 formations from around the world. Formations that have yielded articulated echinoderms are unequally distributed in space and time. Only Laurentia and West Gondwana provide reasonably complete records at the resolution of Stage. The review of the biogeographical distributions of the eight major echinoderm clades shows that faunas from Laurentia and Northeast Gondwana (China and Korea) are distinct from those of West Gondwana and Southeast Gondwana (Australia); other regions are too poorly sampled to make firm palaeobiogeographical statements. Analysis of alpha diversity (species per formation) shows that diversity rose initially to Cambrian Stage 5, declined into Guzhangan and Paibian before returning to Stage 5 levels by the end of the Cambrian. This pattern is replicated in Laurentia and West Gondwana. We show that taxonomically diagnostic ossicles found in isolation typically occur significantly earlier than the first articulated specimens of the same taxa and provide important information on the first occurrence and palaeobiogeographical distribution of key taxa, and of the phylum as a whole.

Supplementary material: Articulated Cambrian echinoderms and Isolated plates of Cambrian echinoderms are provided at: http://www.geosoc.org.uk/SUP18668

The Cambrian represents a crucial period in the evolution of many groups of Metazoa, and echinoderms are no exception. During this period, echinoderms made their first appearance in the fossil record and underwent their initial diversification that established many of the major lines of the later Paleozoic. The existence of putative Ediacaran (Late Neoproterozoic) echinoderms (i.e. Arkarua: Gehling 1987; David et al. 2000) remains speculative and far from widely accepted. As a result, the oldest undisputed members of the Phylum Echinodermata, based on articulated specimens, are from Cambrian Stage 3 and represented by helicoplacoids and edrioasteroids in Laurentia and by gogiid blastozoans in Gondwana. Because of their sturdy calcitic skeleton, echinoderms have left a rich fossil record; however, complete and articulated specimens are typically to be found associated with very specific facies in ‘echinoderm Lagerstatten’ (Smith 1988). Our knowledge of Cambrian echinoderm Lagerstatten has been greatly improved in the last two decades, with many new occurrences reported from palaeogeographical areas where few if any echinoderms had been previously documented, notably in East Gondwana (e.g. China, Korea), West Gondwana (e.g. Morocco, Spain and Wales), and Siberia.

Despite this improved knowledge, facies from which echinoderm remains have been reported remain unequally distributed through time and space, and thus the fossil record of early echinoderms suffers from a strong sampling bias that could confound the analysis of the Cambrian echinoderm palaeobiogeography. Figure 13.1a tabulates the chronological distribution of the 65 formations known to have yielded 188 species of articulated or partially articulated Cambrian echinoderms. The distribution of formations is clearly patchy, with only North America providing an unbroken record of fossiliferous formations through the Cambrian. West Gondwana is the next best-sampled region, albeit

with European localities providing a more complete record than North Africa. Particularly poorly sampled are Siberia, Baltica and some Gondwanan regions, such as South America and the Arabian margin. While Siberia and South America are undoubtedly poorly explored and undersampled, others, such as Baltica and Avalonia, lie in geologically well-studied regions of the world; the dearth of echinoderm-bearing formations in these two regions probably reflects something other than simple sampling bias.

Taking all palaeocontinents together (Fig. 13.1b), it is clear that echinoderm-bearing formations are much more common in Cambrian Stage 5 and Drumian, whereas they are particularly poorly represented at the start of the Furongian. This must partially reflect major retrogradational–progradational shifts over the continental blocks (megacycles; Spencer & Demicco 2002, fig. 1). Comparing the pattern of fossil-bearing formations from the two best-sampled regions (Laurentia and West Gondwana; Fig. 13.1c), we see that a similar bias exists in both regions, but with a better Furongian record in Laurentia. In western North America this pattern is also reflected in a shift in echinoderm bearing facies from fine-grained siliclastics to shelf storm-dominated carbonates (Sumrall et al. 1997). Most notably, the number of species recorded through this time interval shows a strong correspondence to sampling patterns (Fig. 13.1d, e).

With these difficulties in mind, the aim of this collaborative project is to produce the most up-to-date documentation and analysis of the palaeobiogeographical distribution of Cambrian echinoderms, drawing together all published and available unpublished data that are known to us. Furthermore, we have tried to incorporate all sources of information up to June 2011, focusing not just on articulated fossil occurrences, but also including the frequently overlooked record of isolated plates obtained after limestone etching. Particular attention has been devoted to establishing the palaeobiogeographical distribution of first occurrences of the major echinoderm clades in the fossil record.

Palaeogeographical units and chronostratigraphical nomenclature

As outlined in Álvaro et al. (2013), the tectonostratigraphical units into which we place Cambrian echinoderms represent a mixture of palaeogeographical and palaeobiogeographical areas. The tectonostratigraphical units that we employ here are: Baltica, Laurentia (including Sonora, Mexico), the Siberian Platform, West Gondwana (Avalonia, the Mediterranean region (from West to East: Morocco, Ossa–Morena, Iberia, Montagne Noire, Sardinia, Saxo-Thuringia and Bohemia) and its transition to the Arabian margin (Jordan and Turkey)) and East Gondwana (Iran, South China and Australia). For our biogeographical analyses of echinoderm distribution we arbitrarily separate West Gondwana into North Africa and Europe, and the Arabian margin and East Gondwana into the Near East (Turkey and Iran), Far East (China and Korea) and Australia.

Only the Terreneuvian and Furongian of the proposed four-fold Series division of the Cambrian System have been defined by the International Subcommission on Cambrian Stratigraphy and ratified by the International Union of Geological Sciences (Peng et al., 2005).
et al. 2004; Landing et al. 2007; Peng & Babcock 2008). The two series remaining to be defined are provisionally termed Cambrian Series 2 and 3. A tentative global correlation chart is given in Figure 13.2, summarizing the regional chronostratigraphical nomenclature followed in this chapter.

Palaeogeographical distribution of Cambrian echinoderms

The supplementary material to this paper lists all reported echinoderm occurrences from the Cambrian, along with their age and distribution with reference to major palaeobiogeographical areas. During the Cambrian, echinoderms diversified, giving rise to eight major groups (Figs 13.3 & 13.4): (1) helicoplacoids; (2) eocrinoids; (3) edrioasteroids; (4) rhombiferans; (5) cinctans; (6) ctenocystoids; (7) solutans; and (8) stylophorans. This diversity coincides with the Cambrian groups classically identified in the literature (e.g. Ubags 1971, 1975; Derstler 1981; Paul & Smith 1984; Smith 1988; Sprinkle 1992). However, there are several notable differences from these earlier works. First, we now include rhombiferans as members of the Cambrian biota, whereas traditionally they have not been reported before the Early Ordovician. Several recent finds suggest that basal members of this group appeared by Cambrian Series 3 (Ubags 1998; Zamora 2010; Zamora & Smith 2012). Second, two problematic taxa, Echmatocrinus and Eldonia, are omitted here. The putative crinoid affinities of Echmatocrinus remain controversial; this lightly skeletonized fossil was originally described as a primitive Cambrian crinoid (Sprinkle 1973), but later reinterpreted as an octocoral (Ausich & Babcock 1998; Reich 2009). Sprinkle & Collins (1998, 2011) compared these two interpretations, and argued that a basal crinoid assignment is much more likely than an early octocoral assignment, but the discussion is still open. Several species of Eldonia have been interpreted as pelagic sea cucumbers (Walcott 1911; Durham 1974; questionably by Sprinkle 1992), whereas Paul & Smith (1984) and Reich (2005) strongly disagreed with this assignment (Reich 2010). Ossicles of Holothuroidea from middle and upper Cambrian strata were mentioned by Bell (1948) and Mankiewicz (1992), but without description and distinct record and thus remain questionable (Reich 2010). Recently, hemichordate affinities were proposed for Eldonia and allied forms (Caron et al. 2010). Finally, echinoderm affinities have been suggested for the vetulocystids from the Cambrian Series 2 Lagerstätte of Chengjiang, China (Shu et al. 2004, 2010). However, these fossils lack plating and are probably better interpreted as close relatives of vetulicilians and thus as possible stem group deuterostomes (Smith 2004; Swalla & Smith 2008; Clausen et al. 2010). Most of these problematic taxa are restricted to single localities and horizons (Eldonia is an exception), so their exclusion here makes little difference to our subsequent palaeobiogeographical analyses and discussion.

Each group of Cambrian echinoderms is reviewed separately below, with comments on their palaeogeographical distribution.

Helicoplacoidea

Helicoplacoids are a relatively small clade of exclusively Cambrian Series 2 echinoderms. They have a spirally plated, spindly- to bulb-shaped theca (Fig. 13.3a) constructed from numerous rows of interambulacral plates and just three ambulacra (Durham & Caster 1963; Sprinkle & Wilbur 2005). The mouth is thought to be situated at mid-height on the lateral side, and the anus at the distal pole (Derstler 1981; Paul & Smith 1984; Sprinkle & Wilbur 2005; Smith 2008). Helicoplacoids probably lived with one of the thecal poles (the one opposite the anus) either inserted into relatively firm, stabilized substrates (Dornbos 2006) or attached to bioclasts on these substrates (Sprinkle & Wilbur 2005).

The three currently valid genera of helicoplacoids, Helicoplas, Polyplacus and Waucobella (Durham 1967; Wilbur 2006), all come from Laurentia (western USA). A helicoplacoid specimen was reported from central British Columbia, Canada (Durham 1974; questionably by Sprinkle 1992), whereas Paul & Smith (1984) and Reich (2005) strongly disagreed with this assignment (Reich 2010). Ossicles of Holothuroidea from middle and upper Cambrian strata were mentioned by Bell (1948) and Mankiewicz (1992), but without description and distinct record and thus remain questionable (Reich 2010). Recently, hemichordate affinities were proposed for Eldonia and allied forms (Caron et al. 2010). Finally, echinoderm affinities have been suggested for the vetulocystids from the Cambrian Series 2 Lagerstätte of Chengjiang, China (Shu et al. 2004, 2010). However, these fossils lack plating and are probably better interpreted as close relatives of vetulicilians and thus as possible stem group deuterostomes (Smith 2004; Swalla & Smith 2008; Clausen et al. 2010). Most of these problematic taxa are restricted to single localities and horizons (Eldonia is an exception), so their exclusion here makes little difference to our subsequent palaeobiogeographical analyses and discussion.

Each group of Cambrian echinoderms is reviewed separately below, with comments on their palaeogeographical distribution.

Helicoplacoidea

Helicoplacoids are a relatively small clade of exclusively Cambrian Series 2 echinoderms. They have a spirally plated, spindly- to bulb-shaped theca (Fig. 13.3a) constructed from numerous rows of interambulacral plates and just three ambulacra (Durham & Caster 1963; Sprinkle & Wilbur 2005). The mouth is thought to be situated at mid-height on the lateral side, and the anus at the distal pole (Derstler 1981; Paul & Smith 1984; Sprinkle & Wilbur 2005; Smith 2008). Helicoplacoids probably lived with one of the thecal poles (the one opposite the anus) either inserted into relatively firm, stabilized substrates (Dornbos 2006) or attached to bioclasts on these substrates (Sprinkle & Wilbur 2005).

The three currently valid genera of helicoplacoids, Helicoplas, Polyplacus and Waucobella (Durham 1967; Wilbur 2006), all come from Laurentia (western USA). A helicoplacoid specimen was reported from central British Columbia, Canada (Durham 1993), but it is now missing (Wilbur 2006); other undescribed material from here exists (Sprinkle, pers. obs. 2010). Helicoplacoids are also known in the Cambrian Series 2 of Sonora, Mexico (Zamora & Clausen, pers. comm.).

<table>
<thead>
<tr>
<th>GLOBAL</th>
<th>LAURENTIA</th>
<th>S CHINA</th>
<th>AUSTRALIA</th>
<th>SIBERIA</th>
<th>BALTICA</th>
<th>MOROCCO</th>
<th>SPAIN – FRANCE</th>
<th>AVALONIA</th>
</tr>
</thead>
<tbody>
<tr>
<td>FURSIAN</td>
<td>9-10</td>
<td>Ordovician’</td>
<td>Sunwastian</td>
<td>Taoyuanian</td>
<td>Datsionian</td>
<td>Paytonian</td>
<td>Iverian</td>
<td>Khos-Nelegerian</td>
</tr>
<tr>
<td>3</td>
<td>Marjuman</td>
<td>Liupian</td>
<td>Wangcunian</td>
<td>Undian</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Delarman</td>
<td>Wulogian</td>
<td>Taijingen</td>
<td>Floran &amp; upper Templometlan</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Stages 3-4</td>
<td>Yichuan</td>
<td>Nangao</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 2 +</td>
<td>Yichuan</td>
<td>Nangao</td>
<td>Nangao</td>
<td>Toiyanian</td>
<td>Botomian</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 13.2. Correlation chart of the Cambrian showing the global chronostratigraphical series and stages compared with regional usage in major areas of the world; modified from Peng et al. (2004), Landing et al. (2007) and Peng & Babcock (2008). *Siberian regional ‘horizons’ not yet officially erected for the Furisiang.
Of the eight Cambrian echinoderm groups, helicoplacoids are the clade with both the shortest stratigraphical range (restricted to Cambrian Stage 3) and the most restricted palaeobiogeographical distribution (western Laurentia).

**Edrioasteroidea**

Edrioasteroids are an extinct group of sessile forms with a globular to discoidal theca lacking exothecal appendages (Fig. 13.3f, j, k). They have five ambulacra arranged in a 2−1−2 pattern around a central mouth, with the anal pyramid situated orally between the C and D ambulacra. Edrioasteroids first appeared in Cambrian Stage 3 of Laurentia (Durham 1967). The oldest named species is *Stromatocystites walcotti* from Stage 4 of Newfoundland (Schuchert 1919; Smith 1985; Zhao et al. 2010). Other occurrences from the same stage that may be approximately coeval or slightly younger are *Stromatocystites reduncus* and *Edriodiscus primoticus* (Smith & Jell 1990) from the Cambrian Series 3 of Spain. Like many other echinoderm groups, edrioasteroids were much more diverse in Cambrian Series 3.
taxa (with a fully plated aboral surface and biserial flooring plates) occur in West Gondwana (Fig. 13.3j). Stromatocystites has been found in Australia, Bohemia, Morocco, Spain and Turkey (Pompeckj 1896; Jell et al. 1985; Smith & Jell 1990; Lefebvre et al. 2010), as well as in Baltica (Dzik & Orłowski 1995). The closely related genus Cambraster has been reported from Australia, France and Spain (Jell et al. 1985; Smith 1985; Zamora et al. 2007b). Totiglobus is the Laurentian counterpart of Stromatocystites and Cambraster, but represents a distinct clade with very reduced secondary cover plates, a more domed theca and no epispires (Bell & Sprinkle 1978; Sprinkle 1985). A third clade of edrioasteroids, with quadrserial flooring plates, an uncalcified aboral surface and pedunculate zone, is present in both North America (Walcottidiscus) and China (Kailidiscus, Fig. 13.3k; Smith 1985; Zhao et al. 2010). The oldest members of the Order Isorophida (with uncalcified aboral surface and uniserial flooring plates) are known from West Gondwana, where they are represented by the genus Protorophus (Fig. 13.3f) and an indeterminate taxon, both from Cambrian Stage 5 of North Spain (Zamora & Smith 2010). Finally, the fossil record of isolated plates assigned to edrioasteroids (Kouchinsky et al. 2011, in press) suggests this group was in Stages 3 (Kouchinsky et al. in press) and 5 (Kouchinsky et al. 2011) of Siberia, although no articulated specimens have yet been described.
The Furongian record of edrioasteroids is, by comparison, extremely poor and includes only a handful of species. However, the little available evidence suggests that edrioasteroids continued to diversify through the Furongian. Only four edrioasteroids have been recorded so far from the Furongian: one indeterminate edrioasteroid from North America (Sumrall et al. 1997), a possible stromatocystid from China (Ubaghs 1998) and two isocrinoids from Australia, Chatsworthia and Hadrodiscus (Smith & Jell 1990), both of which have un plated aboral surfaces. Finally, edrioblastoids (a derived clade of edrioasteroids) first appeared in the Furongian (Fig. 13.3d); they have been reported so far only from Australia (Cambroblastus enbilatarius; Smith & Jell 1990).

Eocrinoids

The ‘Class’ Eocrinoida is a paraphyletic assemblage comprising stem-group members of most other blastozoan clades (Ubaghs 1968a; Sprinkle 1973; Smith 1984; Paul 1988; Sumrall 1997; David et al. 2000). The body of eocrinoids generally consists of a stalk (Fig. 13.3b); a stalk-like form that enclosed the main visceral, the feeding appendages (brachioles) and an aboral stalk or stem used for attachment and to elevate the theca above the sea floor. In the most primitive taxa (e.g. Gogia and relatives), this appendage consists of a long, multiplated stalk. In more derived forms (e.g. Ubaghisycistis) it is a columnar-bearing stem. This aboral appendage is absent in other taxa (e.g. Lichenoides). Simple respiratory structures (epispires) occur frequently, more or less extensively, over the theca of eocrinoids (Fig. 13.3b, c). The presence of epispires is a pleiomorphic feature within echinoderms, which is lost in more advanced eocrinoids and other blastozoans.

Eocrinoids commonly form the dominant echinoderm group in Cambrian assemblages. The earliest eocrinoids include representatives of the ‘orders’, Imbricata and Gogia. Imbricate eocrinoids are probably the most basal blastozoans (Sprinkle 1973; Paul & Smith 1984). Their stalk is an unorganized, polypolated structure built of numerous imbricate elements (Fig. 13.3c). Cambrian Series 3 imbricate eocrinoids are restricted to Laurentia (North America) where there are just two genera, Lepidocystis and Kinzercystis (Sprinkle 1973). The oldest gogiid eocrinoid is Gogia ojenai from the Stage 4 of Laurentia (Durham 1978). Early gogoids from Gondwana are of approximately the same age as their Laurentian counterparts. They are represented by Alanisycistis and Alanisycistis sp. from the Marianian and Banian stages of South Spain and Morocco, respectively (Ubaghs & Vizcaíno 1990; Nardin & Lefebvre 2005), as well as by Gathzhouneocrinus yui (Fig. 13.3b) and Wudingoeocrinus rarus from Stage 4 of China (Zhao et al. 2007; Hu et al. 2007; Hu & Luo 2008; Luo et al. 2008). Other West Gondwanan occurrences of gogoids are based on isolated plates and their stratigraphical range is comparable to that of articulated specimens. Isolated gogoid plates have been recorded from the Comley of Britain (Series 2; Donovan & Paul 1982), Germany (Elicki & Schneider 1992), from the slightly younger Bembikan Stage of Jordan and North Spain (Clausen 2004; Shinaq & Elicki 2007), and from the Laurentian part of Newfoundland (Skovsted & Peel 2007). Finally, other Cambrian Series 3 eocrinoid skeletal elements are also known from Siberia (Rozanov & Zhuravlev 1992, p. 248; Rozhnov et al. 1992; Kouchinsky et al. 2012, in press).

Eocrinoid faunas from Cambrian Series 3 strata show that basal blastozoans had become more diversified. Imbricate eocrinoids survived, but their only record is from the Fribram-Jince Basin (Vysycistis ubagh; Fatka & Kordule 1990). This region has also yielded a new, as yet unpublished, basal blastozoan, intermediate in morphology between imbricates and gogoids (Nardin 2007). In contrast, gogoids (Fig. 13.3e) are relatively common in siliciclastic platforms of both Laurentia (Mexico and USA; Sprinkle 1973; Sprinkle & Collins 2006; Nardin et al. 2009) and Gondwana (China, Czech Republic, France and Spain; Fatka & Kordule 1984; Ubaghs 1987; Zhao et al. 2008; Zamora et al. 2009; Parsley & Zhao 2010). Some morphological innovations in eocrinoids appeared apparently earlier in West Gondwana than in Laurentia (Zamora 2010). For example, the possession of columnal-bearing stems is documented both in Spain (Ubaghisycistis, Fig. 13.3g; Gil Cid & Domínguez 2002) and in the Príbram-Jince Basin (O. Fatka, pers. obs. 2010) as early as Cambrian Stage 5, instead of the Guzhangian in Laurentia (e.g. Eustycystis; see Sprinkle 1973). This earlier occurrence of holomeric stems in articulated Gondwanan eocrinoids is also mirrored by the fossil record of isolated columnals. Columnals are known from various Gondwanan regions (Australia, Morocco, Sardinia and Turkey) in levels very close to the boundary of Cambrian Series 2–3 (Elicki 2006; Clausen & Smith 2008; Clausen et al. 2009; Gunsburg et al. 2010). They have been also reported from Baltica (Berg-Madsen 1986; Hinz-Schallreuter 2001). Lichenoidoids are a group of stemless eocrinoids that were apparently endemic to West Gondwana (Fig. 13.3i). They are known from Bohemia (Ubaghs 1953) and Spain (Zamora 2010), and related plate taxa (Cymbiocystis and Peridiscus) from the slightly younger Bilbilian Stage of Jordan and Germany (Elicki & Schneider 1992). Other fossil occurrences of Gogia include a new, as yet unpublished, basal blastozoan, intermediate between gogoids and columnal-bearing forms, which is lost in more advanced eocrinoids and other blastozoans.

Rhombifera

Rhombiferans are one of the dominant groups of Ordovician echinoderms (Lefebvre et al. 2013), but the roots of this clade can be traced back into the Cambrian. Unlike their Ordovician relatives, Cambrian rhombiferans lacked specialized respiratory structures (rhombs), and their thecal plates were not standardized into regular rows (Fig. 13.3d). Basal members include a new group called dibrachicystids (Zamora & Smith 2012) bearing two feeding appendages, thecal plates with respiratory folds and a tripartite stem with distal holomeric columnals. Dibrachicystids were originally described from isolated plates (Ubaghs 1973; Sumrall et al. 1997). In the Furongian of Siberia, Sumrall et al. (2003) identified at least six different eocrinoid taxa (including both gogoids and columnal-bearing forms) based on poorly articulated and disarticulated material.
1998; Sdzuy 2000). Finally, Kouchinsky et al. (2011, fig. 38A–F) described a series of isolated plates from the Drumian Stage of Siberia that fit in size and morphology with the proximal stem plates of dibrachycystids.

In the Furongian, more glyptocystitid-like rhombiferans appeared both in Baltica (e.g., Cambrocricus from Poland; Dzik & Orłowski 1993) and Gondwana, such as Australia (Ridersia watsonae; Jell et al. 1985) and southern France (Velieuexcystis, Fig. 13.3h, and Barroubicystis; Ubaghs 1998). The widespread distribution of glyptocystitid-like Gondwanan taxa in Furongian times is confirmed by the presence of isolated plates in both Korea and Wales (B. Lefebvre & S. Zamora, pers. obs. 2002, 2011).

Cincta

Cinctans are a small but distinctive clade of Cambrian Series 3 echinoderms. The cinctan skeleton consists of two parts: the main body (or theca) and a posterior appendage (or stele; Fig. 13.4d). The theca is constructed of a ring of large marginal plates, the so-called cinctus. It is dorsally and ventrally covered with two membranes of tessellate plates. The main body orifices are situated in the anterior part of the theca, the mouth piercing the cinctus and the anus piercing the supracentral integument. One or usually two food grooves run laterally around the anterior part of the cinctus. These grooves converge onto the mouth, which is situated in the anterior right part of the cinctus. The stele is a posterior appendage, considered to be a prolongation of the cinctus (Jeffries 1990; Friedrich 1993; Zamora & Smith 2008).

Cinctans apparently underwent rapid evolution within a short time range (Cambrian Series 3; Smith & Zamora 2009), and have a relatively restricted palaeobiogeographical distribution (West Gondwana and Siberia). They have not been reported from either Baltica or Laurentia. The oldest undisputed cinctan remains correspond to isolated plates from the Leonian (Stage 5) Mansilla Formation (Iberian Chains, Spain). The oldest named species is Protocinctus mansillaensis (Rahman & Zamora 2009) from the same formation, but slightly younger beds (upper Leonian). The Czech species ‘Astericytis’ haviliceki is probably also of similar age (late Leonian), although a precise stratigraphical correlation remains difficult to establish between Bohemia and Spain (Fatka & Kordule 1985), France (C. smithii; Ubaghs 1987) and Wales (Pembrocystis gallica; Domínguez Alonso 2004). Undescribed cinctoid species are known in both Morocco (S. Clausen pers. ob. 2011) and northern Spain (Cinctocystis sp. and Eocticystis sp.; Zamora 2011). Cincto-cystoids with a single-plated marginal ring are restricted to West Gondwana. They were originally reported from Cambrian Stage 5 of southern France (Montagne Noire; Courtessolea moncerorum; Domínguez Alonso 2004; Fig. 13.4k). Courtessolea has been found in Bohemia and Spain but awaits formal description (Zamora 2010; O. Fatka, pers. obs. 2011). A distinctive form, bearing highly reduced thecal plating, occurs in Poland (Jagoszowic; Dzik & Orłowski 1995). Isolated ctenocystoid plates have been reported from Baltica (Sweden; Domínguez Alonso 2004).

Soluta

Solutans are a small, distinct clade of echinoderms that range from the Cambrian to the Early Devonian. They have two unequal appendages, inserted at opposite ends of the body (theca) (Fig. 13.4a). The short, anterior appendage is made from biserial (rarely uniserial) flooring plates and two opposite sets of cover plates. It has been interpreted either as an arm (e.g. Smith 2005) or a brachiole (e.g. David et al. 2000). The long posterior appendage is a stalk-like structure called a stele. In the most primitive genus (Coleicarpus; Fig. 13.4a), the stele is a polyplated, unorganized holdfast. In all other taxa (including the contemporary Castericytis), this appendage is organized into a highly flexible, proximal region and a rigid, distal portion whose plating differs on upper and lower surfaces. The mouth was located at the base of the feeding appendage. In most taxa, both the gonopore and the hydropore are close to the insertion of the feeding appendage. In all solutans, the anus forms a large thecal orifice, opening laterally, and close to the insertion of the stele.

The Cambrian record of solutans is extremely poor, and restricted to Laurentia. Solutans did not appear in Gondwana until the Early Ordovician, and in Baltica until the Mid Ordovician (see Lefebvre et al. 2013). The earliest record of this class is a questionable unnamed and unillustrated form from the Cambrian Series 2 of Pennsylvania (Derstler 1975, 1981). Two genera were described from Cambrian Series 3 deposits of Utah: Coleicarpus and Castericytis (Ubaghs & Robison 1985, 1988; Daley 1995, 1996). Coleicarpus is the most primitive solutan known so far (Daley 1996; David et al. 2000). It attached to skeletal debris on the sea floor and/or to any hard object by its stele. Castericytis is identical in age but has a more derived stele morphology, which was used for attachment only during juvenile stages (Daley 1995). A third unnamed species based mostly on separate stelae was mentioned and illustrated from Cambrian Series 3 deposits in Nevada (Sprinkle 1973, plate 28, fig. 4).
Their Furongian record is limited to two complete but unnamed solutans that were briefly described from northern Alabama (Laurentia) and an unnamed species (Fig. 13.4g), also from Laurentia, described from two isolated steles (Bell & Sprinkle 1980; Sumrall et al. 1997).

**Stylophora**

Stylophorans are an extinct class of echinoderms (Cambrian Series 3–Late Carboniferous), characterized by a bipartite body organization (Fig. 13.4i), consisting of a single appendage and a flattened, fundamentally asymmetrical theca. Their phylogenetic position within the Phylum Echinodermata remains controversial. They may represent primitive, relatively basal echinoderms (Ubaghs 1968b; Smith 2005) or a highly derived clade possibly related to blastozoans (Sumrall 1997) or to arm-bearing echinoderms (e.g. asterozoans and crinoids; David et al. 2000; Lefebvre 2003). The class Stylophora is traditionally subdivided into two orders, Cornuta (Jaekel 1901) and Mitrata (Jaekel 1918). The cornutes (Cambrian Series 3–Late Ordovician) have a relatively rigid appendage, and a generally light, delicate theca framed by narrow marginal plates, whereas the mitrates (Furongian–Late Carboniferous) have a comparatively more highly flexible distal appendage and a more massive theca made from enlarged and thickened marginals and centrals (Lefebvre 2001).

Stylophorans first appeared in Cambrian Series 3. The oldest and most primitive members of the class are heavily plated (‘armoured’) Ceratocystis-like taxa (Fig. 13.4i), which were apparently adapted to relatively warm to temperate, shallow waters (Lefebvre 2007). These basal stylophorans were restricted to Baltica and West Gondwana. In Baltica, Ceratocystis-like taxa are represented by isolated plates from Denmark (Berg-Madsen 1986) and several complete, fully articulated specimens from Sweden (B. Lefebvre, pers. obs. 2009). Armoured stylophorans are much more abundant in West Gondwana, where they have been reported from Bohemia (Pompeckj 1896; Jaekel 1901; Bather 1913; Ubaghs 1967; Jefferies 1969), southern France (Ubaghs 1987), Germany (Sdzuy 2000; Rahman et al. 2010), Morocco (Clausen & Smith 2005), Sardinia (Loi et al. 1995), Spain (Gil Cid & Domínguez Alonso 1998; Zamora 2010) and Wales (Jefferies et al. 1987). Like cinctans and several clades of trilobites, the armoured stylophorans disappeared before the Furongian, probably as a consequence of habitat loss related to a global regression (Zamora & Álvaro 2010).

The first cothurnocystid cornutes appeared slightly later, although still in Cambrian Series 3, and are found in what were once soft substrates deposited in relatively deep, quiet environments (Lefebvre 2007). Cothurnocystids were thus probably ‘psychrospheric’ (cold water-adapted) taxa, with a near-cosmopolitan distribution. They have been reported from western Laurentia (e.g. Archaeocotylus bifida, Ponticulocarpus robisoni; Ubaghs & Robinson 1988; Sumrall & Sprinkle 1999), Siberia (Ponticulocarpus sp.; S. Rozhnov, pers. obs. 2002) and Gondwana, such as Iran (Ponticulocarpus sp.; S. Rozhnov, pers. obs. 2002) and Spain (Zamora 2010).

The Furongian record of stylophorans is relatively rich compared with that of most other echinoderm groups. Although still insufficiently documented, this time interval marks a major turnover in stylophoran assemblages. Cothurnocystid cornutes are the dominant and most diverse Furongian stylophorans (Fig. 13.4i). Their distribution is near-cosmopolitan, with occurrences reported from Laurentia (e.g. Cardiocystella prolizosa; Sumrall et al. 1997, 2009) and various Gondwanan regions such as South China (Han & Chen 2008), southern France (Ubaghs 1998) and Korea (e.g. Sokkaejaecystis serrataa; Lee et al. 2005). The Furongian interval also has recorded the first occurrences of several new clades of stylophorans. For example, Drepanocarpos australis (Australia; Smith & Jell 1999) is the oldest and most primitive known member of hanusiid cornutes (Lefebvre 2001, 2007). Mitrates, long thought to originate in the Early Ordovician, are now known to extend back at least to the Furongian. The heavily plated stylophoran Lobocarpus vizcainoi (Fig. 13.4h) from southern France (Ubaghs 1998) has been reinterpreted as a possible basal mitrate (Lefebvre 2000, 2001), while isolated plates of peltocystids and several fully articulated specimens of primitive mitrocystitids close to Chinianocarpos and/or Vizcainocarpus are now known from Korea (Lefebvre 2007) and South China (B. Lefebvre, pers. obs.).

**The conspicuous record of disarticulated echinoderm ossicles**

Until recently, our understanding of echinoderm diversity and evolution was based almost entirely on analysis of the distribution of well-preserved, articulated specimens. These, however, come predominantly from relatively deep-water palaeo-environments below storm-wave base, where taphonomic conditions were more favourable for such preservation. Because the distribution of articulated specimens is possibly taphonomically biased, an important and possibly more complete record of echinoderms is provided by isolated plates, as these are much more commonly encountered than articulated specimens in a much wider range of palaeo-ecological settings (Fig. 13.5, see Supplementary material).

---

**Fig. 13.5.** Representative Cambrian isolated plates (scanning electron microscope photographs). (a, e) Uniserial element from the Cambrian Series 2 of Siberia (SMNH X 4047). (b, c) Stem columnals from the Cambrian Series 3 of Sardinia (FG 535/4_3, FG 535/4_5). (d) Epispiral bearing plate from the Cambrian Series 3 of Jordan (FG 619/7_115). (f, g) ‘Eocystis’ proximal stem plate from the Cambrian Series 3 of Siberia (SMNH X 4016). (h) Ambulacrual flooring plate from the Cambrian Series 3 of Siberia (SMNH X 4046). Abbreviations: SMNH, Swedish Museum of Natural History, Stockholm (Sweden); FG, Geological Institute of the Technische Universität Bergakademie Freiberg (Germany).
Some Cambrian limestones are packed full of echinoderm elements, and those preserved as iron oxide, glauconite, phosphate or silica replacements can be isolated and studied in 3D after acid etching (e.g. Berg-Madsen 1986; Clausen & Smith 2005, 2008). Preliminary investigation of how isolated skeletal elements from Cambrian limestones are distributed in space and time suggests that they provide important additional information. The study of isolated elements enhances our understanding of echinoderm palaeobiogeography in two major ways.

1. Echinoderm plates with their distinctive stereom structure are easily identified from polished rock sections, and their appearance in the rock record provides evidence of when echinoderms first appeared across different palaeobiogeographical regions. Figure 13.6 summarizes the first occurrence of echinoderm plates in the rock record in five major palaeobiographical regions. In two of the five regions, isolated echinoderm plates have been found in significantly to slightly older deposits than those yielding articulated specimens. This tabulation (Fig. 13.6) demonstrates that the echinoderms first appeared approximately contemporaneously (slightly above the Terreneuvian-Stage 3 boundary) in Laurentia, Siberia and Gondwana, later in the geological record than other phyla, such as arthropods, brachiopods or molluscs (Landing et al. 2010).

2. While the majority of echinoderm plates are non-diagnostic and offer little information other than simply the presence/absence of echinoderms, some are distinctive and taxon-diagnostic (i.e. ctenoidal plates from ctenocystoids, stylocones from stylophorans, marginal frame and opercular plates of cinctans, marginal plates from some edrioasteroids, holocolumnals from eocrinoids or the proximal stem plates from ‘eocystitids’). These can provide important evidence for the occurrence of certain taxa at times or in palaeogeographical regions where no articulated material is known (Fig. 13.6). For example, diagnostic plates from eocrinoids provide the only records we have that members of this group existed in Baltica and Australia during the Cambrian. In Australia, distinctive silicified holocolumnals can be extracted after etching of bioclastic limestones long before the earliest record of articulated blastozoans with holomeric stems. Isolated stylocones in Morocco provide the earliest record of ceratocystid stylophorans in West Gondwana (Clausen & Smith 2005). Finally, numerous localities are known where isolated cinctan marginal plates are abundant yet from where named species have yet to be recorded. Isolated elements can also reveal unexpected diversity, as in the case of the variety of distinct holocolumnal morphotypes found by Clausen & Smith (2008) in Cambrian Stage 5 condensed levels of Morocco. The recognition that many groups appeared earlier in shallow carbonate platforms than in offshore clayey substrates indicates that an important part of the early record of echinoderm evolution from relatively shallow settings is missing.

### Palaeobiogeographical patterns

**First appearances in Laurentia and Gondwana**

Figure 13.6 charts the first occurrence data for our eight echinoderm clades in space and time. Evidence for echinoderms first appears at same time in different palaeocontinents (early Series 2). However, there is a strong endemic constraint in the earliest records, with the first identifiable echinoderms from Laurentia being helicoplacoids and edrioasteroids. Eocrinoids (Imbricata and Gogioda) appeared one stage later. In contrast, the earliest representatives from Gondwana of similar age (Cambrian Stage 3) are gogiid eocrinoids (Alanisicystis from Ossa–Morena and Morocco). Edrioasteroids are present but do not appear in the Gondwanan record until slightly later (?Stromatocystites sp. from Northern Spain and Edriodiscus and Stromatocystites from Australia). Despite these differences, gogiid eocrinoids and edrioasteroids are consistently the first to appear in the fossil record across all regions (Fig. 13.6).

Cinctans, ctenocystoids, solutans, stylophorans and most other groups of radiate echinoderms all appear in Cambrian Stage 5. The clear distinction that exists between these groups right from the very start of their records, and their near synchronicity of appearance, strongly suggests that we are missing the earliest part of their history and that all these groups most likely diverged during

---

**Fig. 13.6.** Table charting the first occurrences of eight major groups of echinoderm in each of five biogeographical regions. The first record of stereom in plates and of holomeric columnals in the rock record is marked.

<table>
<thead>
<tr>
<th>Furongian</th>
<th>West Gondwana</th>
<th>Australia</th>
<th>China &amp; Korea</th>
<th>Siberia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Series 3</td>
<td>6, 7, A 4, 5, 6, 8, Aa</td>
<td>6, a 3, 2, 3'</td>
<td>4, 5, 8, Aa</td>
<td>2</td>
</tr>
<tr>
<td>Series 2</td>
<td>2, 7' 1, 3'</td>
<td>2'</td>
<td>3'</td>
<td></td>
</tr>
<tr>
<td>Terreneuv.</td>
<td>2, 1</td>
<td></td>
<td></td>
<td>2'</td>
</tr>
</tbody>
</table>

**KEY**

- Articulated
- Isolated plates

- helicoplacoids
- eocrinoids
- edrioasteroids
- rhombiferans
- cincta
- ctenocystoids
- solutans
- stylophorans
- Holomeric columnals
- Earliest stereom

---

<table>
<thead>
<tr>
<th>GROUP</th>
<th>Articulated</th>
<th>Isolated plates</th>
</tr>
</thead>
<tbody>
<tr>
<td>helicoplacoids</td>
<td>1</td>
<td>2'</td>
</tr>
<tr>
<td>eocrinoids</td>
<td>2</td>
<td>2'</td>
</tr>
<tr>
<td>edrioasteroids</td>
<td>3</td>
<td>3'</td>
</tr>
<tr>
<td>rhombiferans</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>cincta</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>ctenocystoids</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>solutans</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>stylophorans</td>
<td>8</td>
<td>8'</td>
</tr>
</tbody>
</table>

CAMBRIAN ECHINODERMS 165

by guest on November 27, 2013http://mem.lyellcollection.org/Downloaded from
Cambrian Series 2 or earlier. Consequently, the order in which groups appear in the fossil record must be treated with caution.

**Biogeographical relationships of echinoderm assemblages**

The closeness of relationships shown by the Cambrian echinoderms can be assessed by analysing the biogeographical distribution of individual clades. Although there is no agreed global phylogeny for all echinoderms, many of the constituent groups are widely recognized and accepted as potentially monophyletic. For example, there has never been any disagreement that cinctans and ctenocystoids form well-defined clades. Each of these clades inhabited one or more biogeographical regions; by analysing the pattern of shared occurrences, the degree of similarity of those regions can be established using Parsimony Analysis of Endemism (Rosen & Smith 1988; Da Silva & Oren 2008).

Here we map the distribution of 21 Cambrian clades (Table 13.1) across seven palaeogeographical regions [Laurentia (USA and western Canada), West Gondwana (Morocco, southern Europe and Bohemia), Far East Gondwana (China and Korea), Australia, Arabian margin (Turkey and Iran), Baltica and Siberia]. The distribution of each clade is summarized in Table 13.1. Figure 13.7 shows the results of a Parsimony Analysis of Endemism carried out under Dollo Parsimony (which prohibits the same taxon from arising more than once independently in different geographical areas). Only four of these regions (Laurentia, West Gondwana, East Gondwana and Australia) are sufficiently densely sampled to provide reliable patterns; in other, poorly sampled, regions our inability to distinguish between genuine absences from the region and absences from inadequate sampling makes interpretation problematic.

Turning first to the four regions for which we have a moderately good sample, our analysis clearly distinguishes between a pairing of Laurentia and East Gondwana and a pairing of Australia and West Gondwana. Laurentia and East Gondwana both uniquely have lyracystids and kailidiscid edrioasteroids as part of their fauna, while Australia and West Gondwana share isorophids, stomatocystitids and cambrasterids. Baltica has representatives of just three echinoderm clades, one of which is shared with Australia and West Gondwana, and another (lyracystitid-like rhombiferans) shared uniquely with West Gondwana. The Arabian margin of Gondwana has just two clades, the near-cosmopolitan cothurnocystid stylorhophans and one shared with Baltica, Australia and West Gondwana (stomatocystitids). The pairing of the Arabian margin with Baltica is probably a bias of poor sampling as they are united only by implied secondary losses of lineages. Finally, Siberia has representatives of four clades and provides a mixed signal. Stylorhophans are present in Siberia, but these display a near-cosmopolitan distribution. Column-bearing eocrinoids are also present, but these are shared with both Laurentia and West Gondwana and are therefore uninformative. The same

is true for early stylorhophans, a taxon that Siberia shares with West and East Gondwana, as well as with Australia. However, Siberia uniquely shares with West Gondwana the presence of cinctans, suggesting that the Siberian echinoderm fauna may be closer to that of West Gondwana and Australia than to that of Laurentia and East Gondwana.

Laurentia has the longest branch of any region, possibly reflecting the better sampling available there. Four of the six endemic clades in our analysis come from Laurentia.

**Alpha diversity in space and time**

The Cambrian fluctuations of echinoderm diversity is partly driven by the distribution of appropriate facies where echinoderms have been preserved as articulated specimens (Smith 1988; Zamora & Álvaro 2010) and in part by important ecological changes (i.e. the so-called Cambrian Substrate Revolution; Dornbos 2006; Zamora et al. 2010). This means that a direct reading of the fossil record may inform us just as much about sampling in space and time as it does about echinoderm evolution. A simple plot of the raw data (Fig. 13.1d, e) might be taken to imply that Cambrian Series 3 was a time of palaeobiogeographical expansion for many echinoderm classes, while the

---

**Table 13.1. Distribution of 21 Cambrian echinoderm groups in seven palaeogeographical regions**

<table>
<thead>
<tr>
<th>Major clades</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
<th>19</th>
<th>20</th>
<th>21</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laurentia</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Baltica</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>West Gondwana</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arabian margin</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Siberia</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>East Gondwana (Australia)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>East Gondwana (China and Korea)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Taxa numbered as follows: 1, helicoplacoids; 2, cinctans; 3, solutans; 4, ctenocystoids; 5, ceratocystitid stylorhophans; 6, cothurnocystid stylorhophans; 7, mitrate stylorhophans; 8, primitive glyptocystitid rhombiferans; 9, eocystitid rhombiferans; 10, stomatocystitid edrioasteroids; 11, edrioasterid-like edrioasteroids; 12, isorophid edrioasteroids; 13, imbricate eocrinoids; 14, gogiid eocrinoids; 15, trachelocrinid eocrinoids; 16, lyracystid eocrinoids; 17, column-bearing eocrinoids; 18, cambrasterid stylophorans; 19, primitivly stylorhophans.
Cambrian Series 2 formations typically yield two species, to emerge from this: there are shown in Figure 13.8 and there are several notable features different numbers of echinoderm-bearing formations. The results us to compare diversity patterns across regions that have very alpha diversity (i.e. within formation species richness), and allows number of species recorded from single formations. This measures bias introduced by uneven sampling, we use counts of the Cambrian Series 3 than in lower Furongian strata. To reduce the mixed (carbonate–siliciclastic) environments.

rhombiferans and stylophorans were the dominant groups in Cambrian Series 3 firmgrounds (Zamora Gondwanan faunas that were pre-adapted to such substrates in grounds in Laurentia may have allowed the immigration of (Sumrall stylophorans, with fewer solutans and edrioasteroids, in Laurentia for edrioasteroids (e.g. Stromatocystites) or stylophorans (e.g. Ceratocystis perner)). Furongian communities are dominated by eocrinoids and stylophorans, with fewer solutans and edrioasteroids, in Laurentia (Sumrall et al. 1997). Development of the first carbonate hardgrounds in Laurentia may have allowed the immigration of Gondwanan faunas that were pre-adapted to such substrates in Cambrian Series 3 firmgrounds (Zamora et al. 2010). In France, rhombiferans and stylophorans were the dominant groups in mixed (carbonate–siliciclastic) environments.

However, we know that sampling is possibly much better in Cambrian Series 3 than in lower Furongian strata. To reduce the bias introduced by uneven sampling, we use counts of the number of species recorded from single formations. This measures alpha diversity (i.e. within formation species richness), and allows us to compare diversity patterns across regions that have very different numbers of echinoderm-bearing formations. The results are shown in Figure 13.8 and there are several notable features to emerge from this:

1. Cambrian Series 2 formations typically yield two species, each from its own monotypic level. The Poleta Formation (Cambrian Stage 4) of Laurentia appears to be an anomaly, as it has yielded four species (three helicoplacoids and one edrioasteroid). However, in this case one helicoplacoid and the edrioasteroid (which is known from numerous isolated plates) completely dominate the assemblage and the other two are known only from single specimens. Formations that contain a significant alpha diversity first appeared in Cambrian Stage 3 of West Gondwana where, for the first time, we begin to find as many as eight species represented by numerous specimens and preserved in a single bed (e.g. the Purujosa section; Zamora 2010). This implies that there was a genuine increase in echinoderm diversity going into Cambrian Series 3. Part of the reason why there are so many formations yielding echinoderms in Series 3 is because echinoderms themselves were becoming more abundant and widespread.

2. Lower Furongian formations show diversity levels that are as low as those of the Stage 3, suggesting that there is a genuine drop in diversity at this time. This pattern is repeated in Laurentia, West Gondwana and China. However, we cannot discount the possibility that this drop is because we are sampling a smaller range of palaeo-environments than for other time spans. There is no doubt that in many regions this is an interval characterized by regional regressions which induced the onset of stratigraphical gaps and a record of coarse-grained substrates that precluded the preservation of fossiliferous strata.

3. Later Furongian formations on average have the highest levels of alpha diversity (Fig. 13.8c) of any Cambrian stage in Laurentia, but in West Gondwana and China alpha diversity only returns to match levels achieved in Cambrian Series 2.

Conclusions
The compilation of a complete inventory of fossil echinoderm occurrences throughout the Cambrian comprises records of both articulated specimens and isolated echinoderm plates. Analysis of these data shows that:

1. The Cambrian record of echinoderms spans something like 30 million years. During this time faunas changed compositionally.

2. The distribution of formations yielding fossil echinoderms is not evenly spread through space and time. Siberia, the Arabian margin of Gondwana, South America and Baltica are particularly under-represented and only Laurentia provides an unbroken record throughout the Cambrian.

3. The record of isolated echinoderm plates, although often overlooked, yields important data on echinoderm distribution in space and time. Specifically, it provides the only evidence of eocrinoids from Australia and Baltica.

4. The earliest echinoderms, known from isolated stereom-bearing plates, appear contemporaneously in Laurentia, Siberia and Gondwana.

Fig. 13.8. Echinoderm alpha diversity through the Cambrian based on articulated specimens. (a) Table of mean alpha diversity (average number of species per formation per stage) for six major biogeographical regions (as in Fig. 13.1 colours indicate relative level of alpha diversity). (b) Mean global alpha diversity in the 10 Cambrian stages. (c) Comparison of mean alpha diversity per stage in West Gondwana and Laurentia.
Evidence for a number of groups is first provided by isolated elements, and only later by articulated fossils. Onshore environments, such as shallow-water carbonate platforms, have a comparatively poor record of articulated specimens, and thus our view of echinoderm evolution at this time is biased.

Raw diversity over time points to a major increase in diversity, concentrated in West Gondwana, during Cambrian Stage 5 and to very low diversity levels during the Guzhangian and Paibian. However, analysis of alpha diversity shows that much of this variation may reflect sampling biases, although there is a genuine rise in diversity through the Cambrian in both Laurentia and Gondwana.

 Parsimony Analysis of Endemicity indicates a close relationship between the echi nozzle faunas of Australia and West Gondwana and between those of East Gondwana (China and Korea) and Laurentia. Low sampling in other regions makes interpretation problematic. This work is a contribution to the Projects Consolider MURERO number CGL2006-12975/BTE from MEC and to the project CGL 2010-19491 from MICINN-FEDER. INSU (SYSTER) project PAO2012-786879 “contextes temporaux, environnemental et écologique de l’initiation de l’intervalle glaciaire au Paléozoïque inférieur”, and to the team “Couplages Lithosphère-Océan-Atmosphère” (UMR CNRS-UPS-IRD 5563). This paper is also a contribution of the team ‘Vie Primitive, biosignatures, milieux extrêmes’ of UMR CNRS 5276, ‘Pale´ozoı¨que infe´rieur’, and to the team ‘Couplages Lithosphère-Oce´an-Atmosphére environnemental et e´cologique de l’initiation de l’intervalle glaciaire au Pale´ozoı¨que’. This paper and C. A. Rushton (London) for his information about the Cambrian of Wales. A. Kouchinsky acknowledges support from the NordCEE project grant DNRF53 to D. Canfield from Danish National Research Foundation (Danmarks Fellestidsselskab) and to the ANR project RALI ‘Rise of Animal Life (Cambrian–Ordovician) – team ‘Vie Primitive, biosignatures, milieux extrêmes’ of UMR CNRS 5276, Pale´ozoı¨que infe´rieur’, and to the team ‘Couplages Lithosphère-Oce´an-Atmosphére environnemental et e´cologique de l’initiation de l’intervalle glaciaire au Pale´ozoı¨que’.

References

Bather, F. A. 1913. Caradocian Cystidea from Girvan.
Berge-Maibren, V. 1986. Middle Cambrian cystoid (sensu lato) stem columnals from Bornholm, Denmark. Lethaia, 19, 67–82.
Fatka, O. & Kordule, V. 1984. Acanthocystiscites Barrandei, 1887 (Eocrinoida) from the Jince Formation (Middle Cambrian) of the Czech Republic.
CAMBRIAN ECHINODERMS


Walcott, C. D. 1911. Cambrian geology and paleontology. II. No. 3. Middle Cambrian holothurians and medusa. Smithsonian Miscellaneous Collections, 57, 42–68.


