

Deconstructing helicoplacoids: reinterpreting the most enigmatic Cambrian echinoderms

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Helicoplacoids, the most enigmatic group of Early Cambrian echinoderms, have a spirally plated, inverted pear- to spindle-shaped theca with numerous interambulacral pleats and a long triradiate ambulacrum. They occur in western Laurentia along with the earliest edrioasteroids and epispire-bearing eocrinoids(?), but unlike these other groups, helicoplacoids do not show pentamerism around a centrally located, upward-facing mouth. It is uncertain where the major body openings were located in helicoplacoids, where new plates were added during thecal growth, and whether helicoplacoids were primitive, pre-pentamerism, stem-group echinoderms or derived, relatively specialized forms that had lost several ambulacra.

We made highly modified, side-layout, plating diagrams of different helicoplacoid species by cutting the theca apart half-way between the spiraling ambulacra, leaving four to six interambulacral pleats on each side. This deconstructed thecal strip resulted in an elongate sigmoid-shaped plating diagram with a long central single or paired ambulacrum that is interpreted as three ambulacral branches (A down, C and D up) around a central mouth on the side of the theca. The unrolled plating diagram resembles an elongate French curve drawing template with nearly parallel sides, a large or small sigmoidal top (where the theca is rounded and the interambulacral pleats converge), and an open deviated bottom, where the interambulacral pleats turn down to a truncated conical base. The two upward-extending ambulacra are only one to two interambulacral pleats apart, which only slightly increases the plating strip width. New interambulacral plates are added at the summit and base, and interambulacral pleats rarely branch elsewhere. New floor and cover plates are added at the top and bottom distal ambulacral tips. If this plating model is correct, the anus (which has still not been identified) should be located near the thecal summit where the C and D ambulacra end, and all imperforate extraxial plating has apparently been lost from the theca.

If upright, spirally pleated helicoplacoids with three ambulacra were derived from attached, domal or pyrgate, pentamerism edrioasteroids, numerous changes must have occurred in the thecal shape, number of ambulacra, and interambulacral areas. These changes either occurred gradually in a sequence, or a single major change (spiralled body form?) caused all the others to rapidly follow. Copyright © 2005 John Wiley & Sons, Ltd.

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1. INTRODUCTION

1.1. *Helicoplacoid features and previous studies*

Helicoplacoids are Early Cambrian, inverted pear- to spindle-shaped, spirally pleated echinoderms, perhaps the most disparate members of the Echinodermata. No other members of the phylum have developed a similar body plan and few homologies connect helicoplacoids to other echinoderm groups. Since their discovery and original descriptions (Durham and Caster 1963, 1966), two papers describing new species have been published (Durham 1967, 1993) along with a short summary and longer dissertation chapter reinterpreting their morphology (Derstler

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1981, 1985); three recent papers have discussed their palaeoecology and likely depositional environment (Bottjer *et al.* 2000; Dornbos and Bottjer 2000, 2001). The relationship of helicoplacoids to other early echinoderms has been discussed by several authors including Ubahgs (1971), Sprinkle (1980, 1992), Paul and Smith (1984), Smith (1988), Sumrall (1996), Mooi and David (1998) and Domínguez-Alonzo (1999), but there is no consensus on where helicoplacoids fit in the echinoderm tree. This partly results from the drastically different body plan of helicoplacoids and the difficulty in finding a suitable mode of growth.

Unlike other echinoderms, helicoplacoids do not show the pentamer (radial) symmetry that is found in many Cambrian and most later echinoderms. Furthermore, the body is wound into a left-handed spiral with no apparent body divisions other than ambulacral and interambulacral areas. Other Early Cambrian groups, including edrioasteroids and eocrinoids, have three regions of thecal plating with different types of growth, designated axial, perforate extraxial and imperforate extraxial (Mooi *et al.* 1994; Mooi and David 1998; Sprinkle and Guensburg 2001). Although Mooi *et al.* (1994, figure 6) grouped helicoplacoids with other primitive echinoderms having all three body regions, helicoplacoids appear to lack the coelom-enclosing and attachment structures of the imperforate extraxial skeleton. This reduced body plan makes phylogenetic interpretation difficult, considering that the basal echinoderm stem group likely possessed all three systems. However, their ambulacral (axial skeleton) construction is quite similar to that of the early edrioasteroids (Paul and Smith 1984; Derstler 1985; Wilbur 2003).

1.2. Occurrence and palaeoecology

Helicoplacoids are found in the shaly upper member of the Poleta Formation (Botomian Stage) of California and Nevada, and equivalent units within the Early Cambrian *Nevadella* trilobite zone (Durham 1993). The carbonate-rich lower Poleta Formation contains archaeocyathids (sometimes developed into mounds or small reefs), unidentified edrioasteroid plates (including distinctive oral frame plates) and possible eocrinoid thecal plates, but no evidence of helicoplacoids or their distinctive plates. These other echinoderms attached to hard substrates, such as skeletal fragments (typically trilobite moults), hardgrounds, or skeletized reef-building organisms, using an attachment disc on the lower theca or on a stalk. Helicoplacoids, although sometimes associated with trilobite fragments, have not been found attached in this manner, despite the reconstruction drawn by Derstler (1985, figure 4-1). This occurrence pattern in shales is consistent with the lower pole of upright helicoplacoids being inserted into a firm muddy substrate (sediment stickers), as advocated by Durham and Caster (1963), Durham (1993), Derstler (1985, in part), Bottjer *et al.* (2000) and Dornbos and Bottjer (2000, 2001). Adaptation to a muddy substrate may have led to torsion of the helicoplacoid test into a tapering lower pole that could more easily be inserted into softer substrates. The test was held together by soft tissues in a manner similar to modern asteroids, resulting in a rather low preservation potential because exposed dead specimens would quickly disintegrate after tissue decay (Derstler 1985; Dornbos and Bottjer 2001). Widely spaced storms are the likely culprit in explaining the preservation of rare complete helicoplacoids (Dornbos and Bottjer 2000, 2001) despite a palaeodistribution along the exposed northwest coast of Laurentia, from the White-Inyo Mountains of eastern California to southeastern British Columbia, Canada (Durham 1993). Complete helicoplacoids were typically uprooted by storms that deposited thin, graded shale beds (Dornbos and Bottjer 2000), transported a short distance, and rapidly buried on their sides before any tissue decay or disturbance by scavengers; less commonly, they were knocked over and buried in place with the lower pole still imbedded in the substrate. Only one possible example of an individual buried upright in life position has been figured (see Durham 1993, figure 8.1).

1.3. Phylogenetic position of helicoplacoids—primitive versus derived

Helicoplacoids are definitely echinoderms: they have a skeleton of sutured calcite plates, the plates show characteristic single-crystal cleavage and stereom, the ambulacra have floor plates and cover plates similar to those of other echinoderms, and the ambulacral floor plates bear sutural pores, implying a water vascular system with tube feet. However, helicoplacoids have many other very specialized or unusual morphologic features, and this makes them anomalous because of their very early occurrence in the echinoderm fossil record. They appear to be too specialized to be closely related to any other later echinoderm group.

Previous workers have proposed two alternative viewpoints about where helicoplacoids fit in the phylogeny and evolutionary history of early echinoderms. Most earlier workers in the 1960s to 1980s, and some more recent ones, have considered helicoplacoids as primitive stem-group echinoderms, an asymmetrical or triradial sister group (or ancestor) that branched off before pentamerism appeared (Durham and Caster 1963, 1966; Durham, 1967, 1993; Ubahgs 1971; Paul 1977; Derstler 1981, 1985; Paul and Smith 1984; Smith 1988; Sprinkle 1992; Domínguez-Alonzo 1999). The arguments that three ambulacra preceded the development of five ambulacra were based in part on the '2-1-2' pattern of ambulacra around the mouth of other primitive echinoderms (Sprinkle 1973; Derstler 1985), and the change from three to five ambulacra on the summit of Cambrian eocrinoids during their early ontogeny (Sprinkle 1973; Sumrall 1996). Helicoplacoids are also one of the three earliest echinoderm groups to appear in the fossil record and have the highest Early Cambrian species diversity of any echinoderm group.

More recently, a few workers have instead proposed that helicoplacoids might be a derived and specialized offshoot from a more primitive echinoderm that already had pentamerism (Mooi and David 1998; Wilbur 2003). Both present authors now belong to this second group. Support for this argument includes the unusual body form of helicoplacoids with helical spirals made up of expandable pleats, mouth on the side of the theca with ambulacra spiralling up and down, the apparent lack of a third body region (imperforate extraxial) present in nearly all other early echinoderms, lack of epispines present in many other early echinoderms, and the possible absence of an anus (very unusual for a suspension-feeding echinoderm). Also, pentamerism edrioasteroids, had already appeared in the lower Poleta Formation (slightly earlier than helicoplacoids) based on characteristic oral frame plates, and many other cases of ambulacral reduction from a pentamerism arrangement have apparently occurred in both Cambrian and later echinoderms (Sumrall 2000; David *et al.* 2000), typically by retaining juvenile characteristics through paedomorphosis.

2. HELICOPLOACOID MORPHOLOGY

2.1. Ambulacral features

The axial skeleton and water vascular system of echinoderms were represented by the ambulacra. A radial water vessel was situated either underneath or above the skeletal plates that formed the food groove. These flooring plates were biserially arranged, with pores allowing for the passage of a single tube foot or ampulla between adjacent floor plates, giving each individual plate the appearance of the letter 'I' (Figure 1D). The food groove was roofed by several series of cover plates, the first of which was arranged in a 1:1 correlation with the flooring plates. These pentagonal plates were overlain by a second, and in some cases a third, series of smaller plates (Durham 1967, 1993; Paul and Smith 1984; Derstler 1985). Durham (1967, 1993) described specimens of *Waucobella* and *Westgardella* with tube foot pores between adjacent cover plates, implying tube foot exposure and therefore no protection while the cover plates were closed. We believe the floor plate series in these specimens was distended during burial, leading to the misinterpretation of these structures as a series of pore-bearing cover plates. Durham (1993, figure 5.4) also showed an internal view of one row of floor plates articulated with the base of a cover plate series, misinterpreted as an internal view of the cover plate series itself.

The ambulacra of helicoplacoids are arranged in a triradial manner, with the junction of the ambulacra in a medial position on the side of the test. The mouth almost certainly was located at this junction (Derstler 1981, 1985; Paul and Smith 1984), because this is the pattern in all other echinoderms that have two to five converging ambulacra. Furthermore, it is unlikely that the mouth was located at the upper pole as proposed by Durham (1993), because the two upper ambulacra nearly always terminate before reaching this pole.

2.2. Interambulacral pleats

Most of the helicoplacoid theca is composed of a series of helically arranged, pleated, interambulacral plates that apparently were able to expand in the manner of an accordion (Figure 1C). Each pleat has a series of thick, rounded or inverted, V-shaped medial plates that project above the test surface, sometimes with pustular or ridged ornament

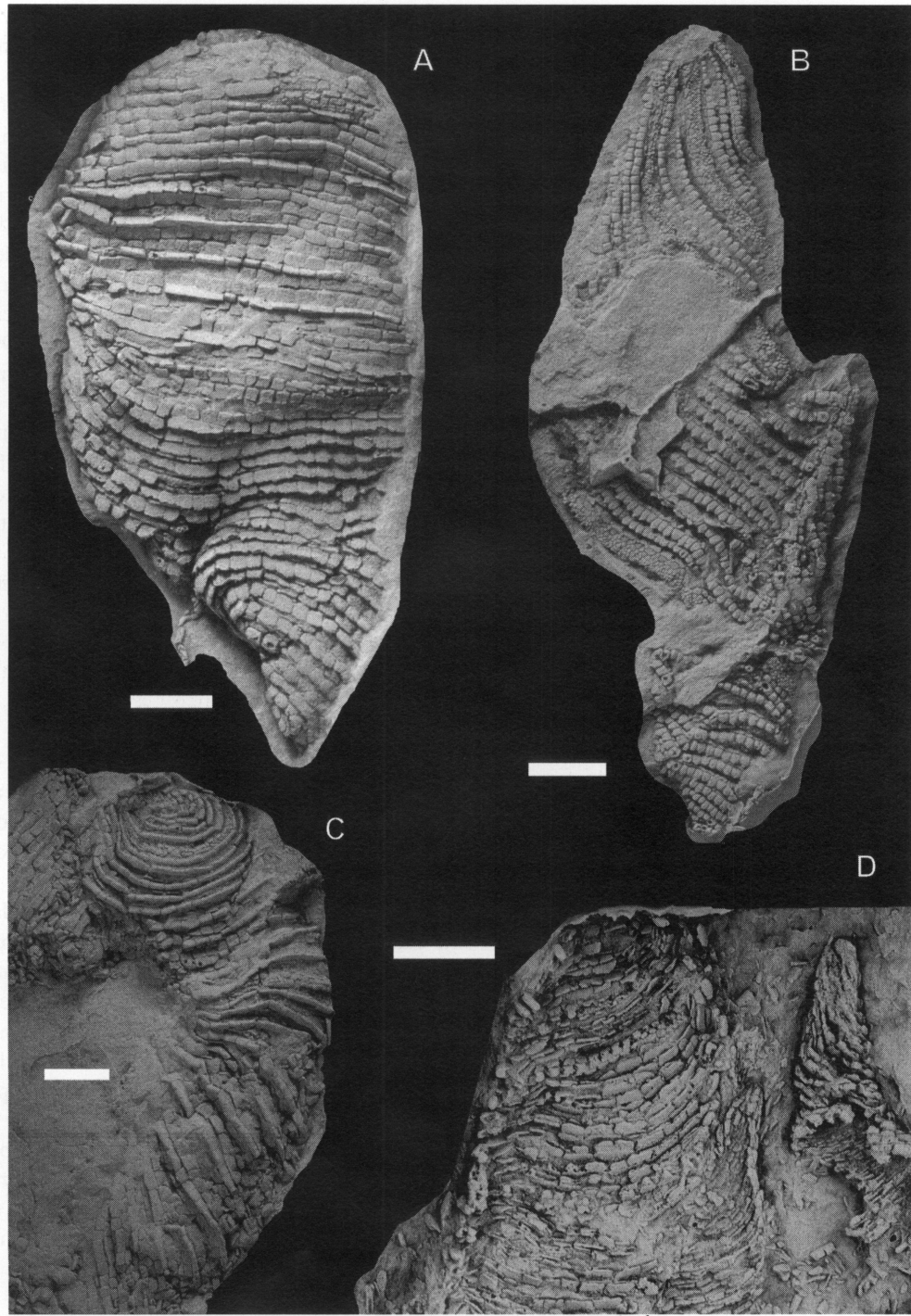


Figure 1. Representative helicoplacoids from the Lower Cambrian Poleta Formation, California and Nevada. (A) *Westgardella blancoensis* Durham, paratype, UCMP 38152, showing elongate pear-shaped theca. (B) *Waucobella nelsoni* Durham, holotype, UCMP 14769, showing spindle-shaped theca. (C) *Westgardella blancoensis* Durham, TMM 2032TX1, rounded upper pole with terminal ambulacrum and expanded medial portion of test below. (D) *Helicoplacus everdeni* Durham, LACMNH 17529, specimen on left showing ambulacral interior with pore-bearing floor plates near top; specimen on right showing tapered lower pole. All specimens are latex or silicone casts of natural moulds coated with ammonium chloride. Scale bars represent 5 mm.

or short spines. These medial plates are accompanied by two depressed series of thinner, rectangular, lateral plates alongside and partly beneath them. The lateral plates were apparently hinged between pleats and could swing outward to expand the test (Durham and Caster 1963; Durham 1967); however, the exact mechanism by which they did so (muscular activity or hydrostatic pressure?) is still unknown. Only larger specimens have been found in the expanded state (see Figure 1A, C), suggesting the ability to expand and contract developed later in ontogeny, perhaps as a response to currents higher in the water column bending the larger theca over (Derstler 1985) or respiratory stress brought on by a decrease in the surface area-to-volume ratio. The interambulacral pleats of helicoplacoids are unique among echinoderms, as is the apparent lack of body openings (sutural pores, hydropore–gonopore? and anus?) through this part of the skeleton. Other Early Cambrian echinoderms, such as *Gogia ojenai* (Durham 1978), *Camptostroma rodnyi* (Durham 1966), and *Stromatocystites* (Paul and Smith 1984; Smith 1986; Smith and Jell 1990), have pores along the interambulacral or thecal plate sutures, allowing for passage of coelomic fluids out to soft bulbs that were most likely respiratory. However, sutural pores may not have been able to develop in a flexible pleated theca, explaining the apparent lack of respiratory structures. Other unidentified body openings, including the hydropore–gonopore and anus (if present), should lie between the closely spaced C and D ambulacra (if these are correctly identified), somewhere between the mouth and the upper pole of the theca.

2.3. Lower and upper poles

The lower pole in nearly all helicoplacoids examined is relatively small, elongate conical, and has only interambulacral pleats turned vertically with the plates diminishing in size distally (Figure 1D). About eight to twelve pleats extend down to the distal tip where the thecal axis is located, or about the number present in a typical interambulacrum. We have not seen plating on the distal tip different from the interambulacral pleats on the side and none of the specimens examined shows lower ambulacrum A extending down onto the lower pole. Typically, that ambulacrum ends above the lower pole at about 25–30% of the thecal height, which may be an indication of the depth to which the lower pole was imbedded in the substrate (Dornbos and Bottjer 2000).

The helicoplacoid upper pole is more variable in size and morphology. In many helicoplacoid species, it is a large rounded dome to the theca, with the interambulacral pleats spiralling into the central axis and ending. The two upward-projecting ambulacra appear to end a short distance (about 10% of thecal height) below the summit in these species (Figure 1C). No other thecal openings (or plate-covered pyramids) have been observed here on well-preserved specimens (see Durham 1993, figures 5.2–5.3, 5.5–5.6). The upper pole in *Waucobella* and small specimens of a few other species are smaller and more conical (Figure 1B), and the ambulacra turn axially upward. First the C? and then the D? ambulacrum dies out just below where the remaining interambulacral pleats decrease in size and then end (Durham 1993, figure 3.1). Small conical summits have been seen only in side view, and again no openings or pyramids have been observed there.

3. MATERIALS AND METHODS

3.1. Museum specimens and field collections

We studied about 50 casts of helicoplacoid types and other well-preserved specimens from several museum collections, and from one amateur collector. We also made new collections of helicoplacoids, totalling about 150 specimens, from the Poleta Formation in Westgard Pass, eastern California, in the late 1980s, June 2000 and June 2001, and from the Poleta Formation in western Nevada in June 2002 and July 2003.

3.2. Making side-layout plating diagrams

Several standardized plating layouts have been used to portray the three-dimensional arrangement of thecal or calyx plates in different echinoderms on a two-dimensional surface. Most commonly used for cylindrical, conical, and sometimes globular echinoderms is a side-layout plating arrangement which cuts the theca vertically along

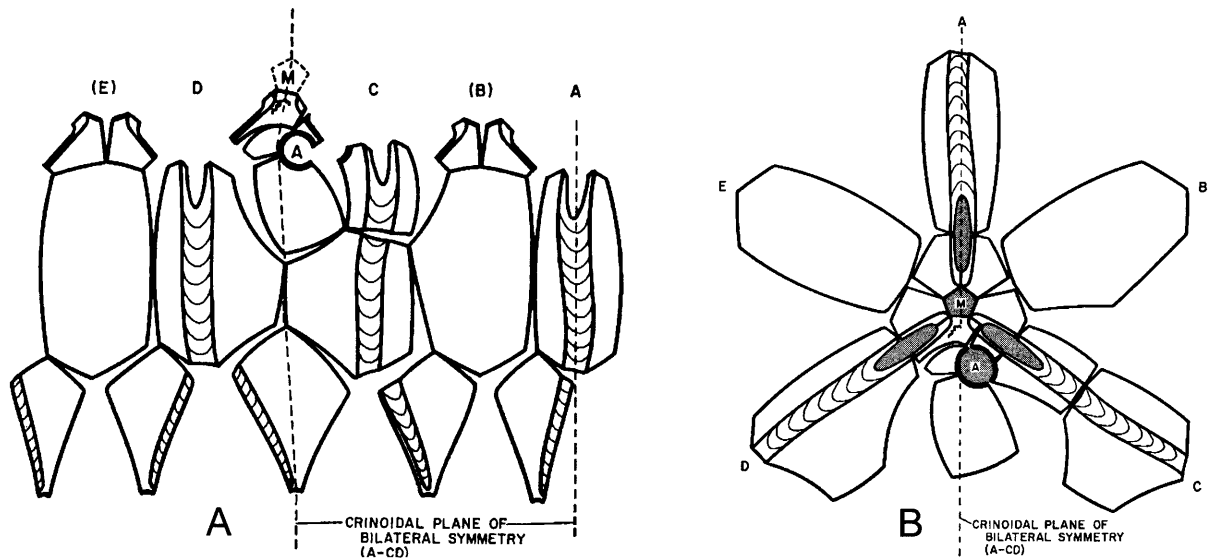


Figure 2. Examples of side- and radial-layout plating diagrams. (A) Standard side-layout plating diagram for the crinoid *Tripatocrinus*. (B) Orally centred radial-layout plating diagram for the crinoid *Tripatocrinus*. Key: A, B, C, D, E = rays radiating from central mouth; stippling = openings into body, including mouth (M) and anus (A, in heavy-lined circle). (A) and (B) modified from Sprinkle (1973, text-figures 3, 4, respectively, reproduced by permission of the Society for Sedimentary Geology (SEPM).

plate sutures (typically through a back interray, often EA) and unfolds the theca from back to front, keeping plates in the widest part of the theca in contact, and putting plates in alternating circlets above and below in contact with plates of the widest circlet but separated from each other (Figure 2A; also see Ubags 1978, figures 71, 88). This plating arrangement emphasizes horizontal alternating circlets in the theca or calyx, a common feature in stemmed echinoderms with reduced thecal plating showing pentameral symmetry.

Another plating layout commonly used in conical or globular crinoids is a radial layout typically centred on the calyx base or stem facet (Ubags 1978, figures 71, 99) that keeps ray plates and plates of each interray together. This is either done as a complete radial array with 360° coverage, or a partial radial array with 180–262° coverage (usually two to four rays and three interrays, including CD). This emphasizes the sequence of ray plates in the cup leading out to the lower arms, and the number and arrangement of interbranchials in the interrays. A few radial arrays in crinoids have been centred on the mouth to emphasize oral structures and ambulacral grooves extending down the cup (Figure 2B) or leading to arms mounted on the radials. Radial plating layouts are also commonly used in echinoids, centred either on the apical system or the mouth.

None of these standardized plating layouts seemed reasonable for helicoplacoids that have helically spiralled plating, lack pentameral symmetry, rays and erect appendages, and apparently have the mouth on one side of the theca. The ambulacra seem to be the key for understanding helicoplacoid morphology and growth. They spiral between 1½ to 2½ times around the theca in most large specimens. Very few specimens show the ambulacra dividing at the mouth plus more than one additional segment on this side either above or below (see Durham 1993, figures 3.1–3.2), implying that the ambulacra die out at or before one complete whorl above or below the mouth. Also, the interambulacral pleats parallel the ambulacra with almost no deviation, implying that these two regions are tied together in some manner, perhaps in their functional morphology and mode of growth. Because of this, we decided to try a highly modified side-layout plating diagram for helicoplacoids, with the cut for unfolding the plating highly oblique following the helical spirals. We cut the plating apart down the middle of each interambulacral area (typically eight to twelve pleats wide), so that the spiralling strip would have one to two central ambulacra and four to six interambulacral pleats on each side.

To do this, we made clay models at about twice natural size representing two commonly occurring thecal shapes in helicoplacoids. We coated these with 1–2 mm of clear latex rubber, which, when dry, had spiralled ambulacra

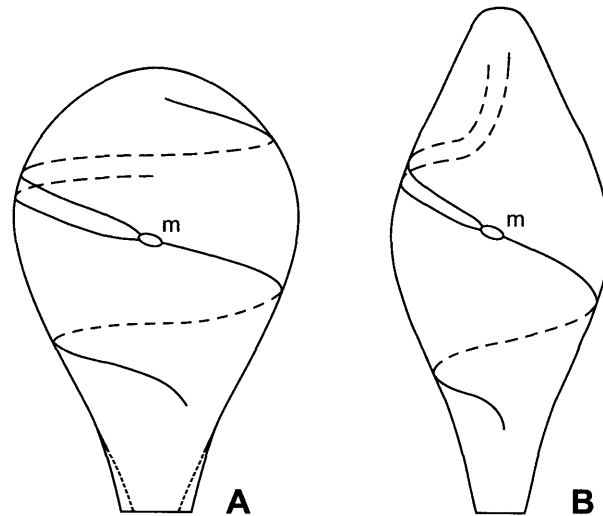


Figure 3. Helicoplacoid model shapes used to construct modified side-layout plating diagrams. (A) Pear-shaped model 1, enlarged. Lower pole of clay model was too wide; dotted lines indicate more reasonable width. (B) Spindle-shaped model 2, enlarged. Key: m = mouth.

and interambulacral boundaries drawn on them in ink before cutting the latex apart with sharp trim scissors. Model 1 was inverted pear-shaped, with a protruding base, widely conical lower theca and an elongate rounded top (Figure 3A). We placed the mouth at 58% of the thecal height from the base, used an 18° ambulacral spiral angle to the horizontal with eight to ten interambulacral pleats between ambulacral segments, and turned the lower ambulacrum vertically down toward the base at about 30% of thecal height and ended it just below. These shape and plate-spiralling specifications for model 1 represent averages from ten well-preserved measured specimens, seven of which were figured in Durham (1993, figures 2, 3, 6, 7) and three of which were newly collected, assigned to helicoplacoid species such as *Helicoplacus everndeni* (Figure 1D), *H. gilberti*, *H. guthi*, *Westgardella firbyi* and *W. blancoensis* (Figure 1C).

Model 2 was more spindle-shaped and thinner, with a long, conical base and summit, and a rounded central portion in between (Figure 3B). We placed the mouth at 60% of the thecal height from the base, used a higher 35° ambulacral spiral angle to the horizontal with twelve interambulacral pleats between ambulacral segments, and turned both the lower and upper ambulacra vertically toward their respective poles at about 25 and 75% of thecal height, and extended them somewhat further. These shape and plate-spiralling specifications for model 2 were based on, or averaged from, four well-preserved measured specimens, including the holotype of *Waucobella nelsoni* (Figure 1B), the Paul and Smith (1984) figured specimen of '*Helicoplacus curtisi*' (see Durham 1993), and two small new specimens of *Helicoplacus* and *Westgardella*.

4. RESULTS

4.1. What the modified side-layout plating diagrams show

The cut-out latex overlay from model 1 produced a narrow S-shaped strip 235 mm long by 34–35 mm wide in the centre, giving a length-to-width (L/W) ratio of 6.7. The two long central ambulacra surrounded on both sides by long, parallel, interambulacral pleats (Figure 4) extended 1.0 whorls above the mouth, and the single ambulacrum below the mouth extended 1.25 whorls, for a total of 2.25 complete whorls. Because the two ambulacral branches above the mouth remain only one to two interambulacral pleats apart, branching of the ambulacra above the mouth does not greatly increase the width of the strip. The top of the theca forms a sigmoidal structure around the thecal axis where the interambulacral pleats spiral to an end (Figure 4). This end of the plating strip closely resembles a

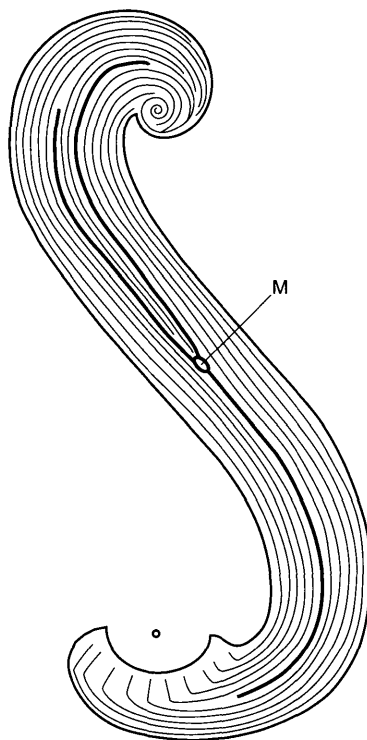


Figure 4. Modified side-layout plating diagram (much enlarged) for helicoplacoid model 1. Note elongate S-shape, long ambulacra (bold), parallel interambulacral pleats, central mouth (M) above which only one to two central pleats are present, and top and bottom ends of spiral axis.

French curve drafting template or one of the sound holes in a violin or viola. The bottom of the theca forms a highly deviated hollow structure where a relatively small number of interambulacral pleats turn down and end in a conical tip. This open deviated structure at the base is much too large in our model 1 (because we were supporting the clay model on this lower pole) compared to its smaller size in actual specimens.

The model 2 latex overlay, based partly on *Waucobella nelsoni* Durham, 1967, produced a shorter, wider, faintly S-shaped strip 193 mm long by 45–46 mm wide in the centre, giving a L/W ratio of 4.2 (Figure 5). The two fairly long central ambulacra extended 0.5 whorls above the mouth before turning up towards the upper pole, and the single ambulacrum below the mouth extended 1.0 whorls before turning down towards the lower pole, for a total of 1.5 complete whorls. Because the upper pole was narrow, only a small sigmoidal deviation was present here (Figure 5), and the deviation for the basal pole was also less pronounced. Most of the differences from Model 1 were apparently produced by the much narrower, conical, upper pole (where the ambulacra turned up) and the higher coiling angle, which together produced fewer complete ambulacral whorls.

Why does the sigmoidal upper end of helicoplacoid model 1 resemble a French curve? After the ambulacra end, the interambulacral pleats gradually terminate one after the other as they approach the spiral axis (see Durham 1993, figure 5, for examples of this). The centre of this spiral typically has small plates from the few remaining pleats, perhaps arranged along a geometric spiral or possibly in a Fibonacci series. French curve rounded ends probably also represent a geometric spiral, terminated as the curvature reaches a small size.

4.2. Ambulacral morphology and growth

The plating strips derived from these two models strongly indicate that the single or paired ambulacra, and their adjacent interambulacral pleats, are closely coordinated in their function and probably in their growth. In agreement with Derstler (1985) and Domínguez-Alonzo (1999), but not Durham (1967, 1993), we interpret the

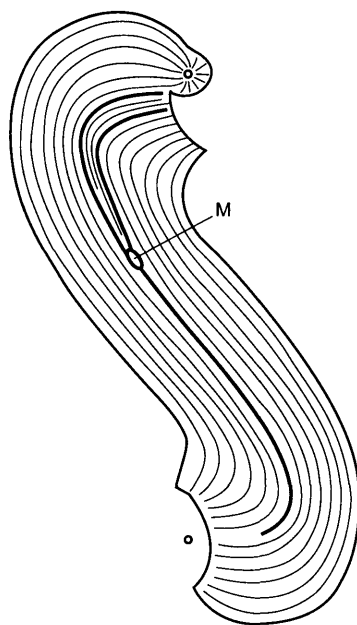


Figure 5. Modified side-layout plating diagram (enlarged) for helicoplacoid model 2. Note less elongate shape, fairly long ambulacra (bold), parallel interambulacral pleats, central mouth (M), and top and bottom ends of spiral axis.

ambulacral system of helicoplacoids as having a lateral mouth on the side of the theca where the ambulacra 'branch'. Three ambulacra lead away from the mouth, here interpreted as closely spaced ambulacra C and D (Derstler (1985) called these B/C and D/E) extending up toward the thecal summit and separate ambulacrum A extending down toward the thecal base. In early echinoderms, A, C and D are the earliest-formed ambulacra in ontogeny, with B and E later branching off C and D, respectively. Ambulacra A, C and D are the ones usually remaining if two ambulacra are subsequently lost (Sprinkle 1973; Sumrall 2000).

Although only three ambulacra are present, these ambulacra are much longer than the five straight or slightly curved ambulacra in most discoidal edrioasteroids. This implies that the total length of ambulacra for food collection and respiration was comparable, or may even have favoured the helicoplacoid arrangement, as pointed out by Derstler (1985). This is one obvious reason why helicoplacoids have developed the helically spiralled design for their thecae; the ambulacra can grow to be very long and face in all directions to intercept food. Each ambulacrum lies within a groove formed by adjacent interambulacral pleats that are parallel to the ambulacrum. If the ambulacra in helicoplacoids obeyed the ocular plate rule (Mooi *et al.* 1994; Mooi and David 1998), as did other early echinoderms, they should have grown outward from the mouth, and the newest ambulacral floor and cover plates should have budded off at the ambulacral tips. The ambulacra would have become increasingly long as the plating strip grew more elongate and the thecal volume increased, thus keeping the helicoplacoid well fed at all sizes.

4.3. Interambulacral pleat morphology and growth

The four to six interambulacral pleats along each side of the ambulacra in the helicoplacoid plating strip provide spacing, flexibility and perhaps expandability to the theca. Although small thecae are usually found with the pleats contracted, large specimens have been found both in the contracted and expanded state (see Figure 1A, C and Durham 1993). The plating strips show that the pleats expand perpendicular to the direction of interambulacral pleat and ambulacrum spiralling which would probably produce less than a few per cent increase in length for a doubling in width. This means that helicoplacoids were able to lean over in the water column to resist currents (Derstler 1985), or perhaps expand their spirally pleated theca for respiration, similar to domal edrioasteroids which could bulge up their oral surface using imbricate interambulacral plates (Sumrall 1994). Tiny

interambulacral plates are rarely found along the length of a pleat, except at the spiralled or pointed ends, so we agree with Derstler (1985) that this is where growth of the interambulacral pleats took place. Therefore, growth of both the ambulacral and interambulacral plating took place at the distal ends of the theca away from the near-central mouth. Also, most interambulacral pleats are continuous from one end of the plating strip to the other, with only a few known cases of new pleats being added or terminated. Right above the mouth, one to two new pleats are added between the two slightly diverging and then parallel C and D ambulacra; just below the mouth, at least one marginal pleat appears to terminate in a newly collected specimen. This would keep the width of the plating strip almost the same from below to above the mouth.

4.4. Have helicoplacoids lost the imperforate extraxial region?

Because helicoplacoids have only ambulacral (axial) and closely associated pleated interambulacral (apparently perforate extraxial) plates making up their theca, they appear to have lost all of the imperforate extraxial plating that is present in other early echinoderms. The only place on the helicoplacoid theca that might represent imperforate extraxial plating is the bottom surface of the lower pole, if it were plated. Unfortunately, this surface is poorly known at present, so it is uncertain what kind of plating, if any, is present here. If this small lower pole were inserted into the sediment, as most authors have proposed, it would not need to have a differently plated lower surface, making the absence of imperforate extraxial plating more likely. The same is true if the anal pyramid were, in fact, located at this pole (proposed by Domínguez-Alonzo 1999).

4.5. Deriving spiralled helicoplacoids from domal edrioasteroids

Helicoplacoids, along with slightly earlier edrioasteroids and eocrinoids(?), are the three earliest echinoderms to appear in the fossil record. The nine named species of helicoplacoids make them the most diverse group of Early Cambrian echinoderms. However, their thecal morphology is so unusual compared to coeval and later echinoderms that we believe they are derived, very likely from domal or pyrgate edrioasteroids, based on their similar plesiomorphic ambulacra. Assuming they are derived and that we have correctly identified the three ambulacra, a large number of changes have apparently occurred in this transition, including at least the following (Figure 6).

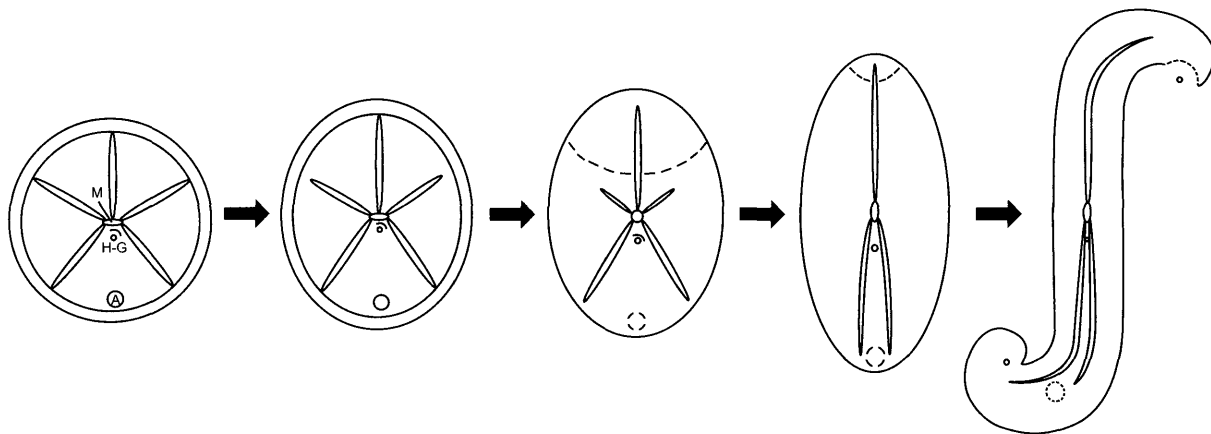


Figure 6. Hypothetical stages in the Early Cambrian morphological transition from a pentamerous, pyrgate, attached edrioasteroid (left) to a tri-radiate, helically spiralled, mud-sticking helicoplacoid (right). Left and left-centre drawings are top views with mouth (M), anus (A) and hydropore-gonopore (H-G) marked, showing attachment rim, beginning of thecal elongation, and shortening of side ambulacra; centre drawing is oblique-top showing continued elongation with even shorter side ambulacra, loss of rim, and reduction of attachment area (curved dashed line at top); right-centre drawing is oblique-side showing even greater thecal elongation, complete loss of side ambulacra, loss of most interambulacral plating between the two lower ambulacra and further reduction of attachment area; right drawing is a side view showing extreme elongation, imposition of helical spiralling and deflection of ends of theca around coiling axis (small circles). Note that the final stage in this transition (right) has the lower (insertion) pole at the top, the opposite orientation from the model 1 plating strip shown in Figure 4.

1. The theca became increasingly elongated along an A–CD symmetry plane.
2. The interambulacral plating changed from adorally imbricate to pleated, with the pleats becoming aligned in the plane of elongation and adding new plates only at their distal ends.
3. As the theca elongated, the two late-developing side ambulacra (B and E) decreased in length and finally disappeared, while the three remaining ambulacra became longer by faster(?) growth at their distal tips.
4. As the theca elongated, ambulacra C and D, that originally had been about 80° apart (slightly wider than other interrays), gradually lost the CD interambulacral plates separating them until they were parallel and only one to two (newly organized) pleats apart.
5. As the theca elongated, the extraxial imperforate lower theca and attachment surface were gradually reduced in size and moved to the A-ray(?) end of the theca, and were eventually lost.
6. At some point in this process, the elongate theca became helically spiralled around an upright central axis, producing an S-shaped plating strip.
7. The animal with its upright spiralled theca developed the ability to insert its tapered lower pole (A ray-end) into the muddy sea floor, instead of attaching to a hard substrate such as a skeletal fragment.

Figure 6 shows these changes as if they occurred in a slow gradual fashion with changes 1–5 occurring in sequence, followed by 6 (and 7); however, this may not have been true. Two of the most interesting questions involving the above changes are in what order did these changes occur and was there a single, perhaps rapid, ‘master change’ that triggered some or most of the others? If helicoplacoids are derived from edrioasteroids (order from left to right), the graded sequence of changes shown by Figure 6 seems most likely. The major candidate for a master change is number 6, the helical spiralling of the theca, possibly from a failure of one side of the theca or a coelomic cavity to develop correctly in metamorphosis. We have shown this change occurring at the end of the sequence, but it might have occurred at the beginning, so that all of the other changes in morphology (1–5) and life mode (7) would have followed to make best use of a distinctly different thecal shape and to develop a new way to live upright on a muddy sea floor. Finally, if helicoplacoids are primitive, as many previous workers have proposed, then changes 1–7 in Figure 6 would have occurred in the opposite direction (order from right to left). We believe this last scenario is unlikely.

5. CONCLUSIONS

1. Helicoplacoids have a spiralled thecal morphology with only three ambulacral branches and pleated interambulacra. We infer that the mouth is lateral at the point where the three ambulacra join, in agreement with Derstler (1981, 1985), Paul and Smith (1984), and Domínguez-Alonzo (1999), but not Durham (1967, 1993).
2. We used a highly modified side-layout plating diagram to better visualize the plating in inverted pear- to spindle-shaped thecae of helicoplacoids. These plating models produced an elongate, slightly to strongly S-shaped, thecal strip having one to two central ambulacra and four to six parallel interambulacral pleats on both sides that resembles a French curve drawing template.
3. Although only three spiraling ambulacra are present in helicoplacoids, they are much longer than the five ambulacra on the domed summit of edrioasteroids, so that the total ambulacral length for feeding and respiration was probably comparable or greater in helicoplacoids.
4. If the ambulacra are correctly identified in these plating models, then the unidentified anus (if present) should be located where the two upward-extending ambulacra (C and D) end near or on the rounded or conical upper pole.
5. Because the sides of the plating strip are nearly parallel and the interambulacral pleats open perpendicular to their sides, the theca can be moderately expanded and contracted without greatly lengthening or deforming the ambulacra.
6. Growth of helicoplacoid interambulacral pleats probably occurred at the upper and lower thecal poles where the pleats decreased in plate size and ended. Almost no tiny interambulacral plates have been found between larger ones, implying no later insertions elsewhere.