ORIGINS AND BIOMECHANICAL EVOLUTION OF 
TEETH IN ECHINODIDS AND THEIR RELATIVES

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Abstract: Echinoid teeth are without doubt the most complex and highly specialized skeletal component to have evolved in echinoderms. They are biomechanically constructed to be resilient and tough while maintaining a self-sharpening point. Based on SEM analysis of isolated tooth elements collected primarily from the Ordovician and Silurian of Gotland, we provide a detailed structural analysis of the earliest echinoderm teeth. Eight distinct constructional designs are recognized encompassing various degrees of sophistication, from a simple vertical battery of tooth spines to advanced teeth with multiple tooth plate series and a reinforced core of fibres. These provide key data from which we reconstruct the early stages of tooth evolution. The simplest teeth are composed of stacked rod-like elements with solid calcite tips. More advanced teeth underwent continuous replacement of tooth elements, as a simple self-sharpening mechanism. Within echinoids tooth design was refined by evolving thinner, flatter primary plates with buttressing, allowing maintenance of a sharper and stronger biting edge. Despite the obvious homology between the lanterns of ophiocistioids and echinoids, their teeth are very different in microstructural organization, and they have evolved different self-sharpening mechanisms. Whereas echinoid teeth evolved from a biseries of mouth spines, ophiocistioid goniodonts evolved from a single series of mouth spines. Rogeriserra represents the most primitive known battery of tooth elements but its taxonomic affinities remain unknown.

Key words: Ordovician, Silurian, echinoderms, functional morphology, stereom.

Amongst the extant classes of echinoderm only sea urchins possess a complex dental apparatus. This structure, commonly referred to as the ‘Aristotle’s lantern’ on account of its resemblance to an antique lamp, comprises 35 skeletal elements and is controlled by 40 sets of muscle (Candia Carnevali et al. 1993). Five teeth, each braced within a pair of skeletal elements, the hemipyramids, protrude through the mouth and are involved in feeding. They are used to slice macroalgae, sea grass and carrion into pieces of a suitable size for ingestion and to rasp encrusting algae and invertebrates off hard substrata. The tips of the teeth converge vice-like and act as a grab to scrape encrusters off the surfaces on which they are attached. In clypeasteroids, teeth do not project out of the test but are used primarily as an internal crushing mill (Ellers and Telford 1991).

Of all the elements that go to make up the skeleton of an echinoid, teeth are by far the most complex and specialized in design at both the macro- and micro-scales. This is because they have evolved biomechanically to withstand the massive compressional, bending and torsional stresses associated with feeding, and to maintain a biting edge that is both hard-wearing and ever-sharp. Because of their high degree of complexity and clear functional design, teeth of extant echinoids have been subject to a number of detailed morphological and biomechanical studies (Märkel and Titschack 1969; Märkel 1970a, 1970b, 1974, 1978; Märkel and Gorny 1973; Märkel et al. 1977; Scally 1980; Jensen 1974, Candia Carnevali et al. 1993; Birenheide et al. 1996; Wang et al. 1997). These studies have highlighted just how supremely well-adapted teeth are for their biological role. There have also been a small number of studies about the teeth of fossil crown group members (Märkel 1978; Smith 1981, 1982; Smith and Hollingworth 1990), and consequently we now have a modest understanding of the evolutionary diversification of teeth over the past 250 Ma. Although teeth of post-Paleozoic echinoids differ most notably in cross-sectional shape, their underlying microarchitectural organization remains basically similar (Text-fig. 1).

Clearly, such an advanced structure must have a long history of development. Yet surprisingly little is known about the morphology of teeth in Paleozoic echinoids. The only papers that describe stem group echinoid teeth are those of Jesionek-Szymańska (1979), Smith (1984) and Boczarowski (2001). These demonstrate that some
teeth were constructed very differently in the early Palaeozoic, but what this signifies in terms of the biomechanical evolution of tooth design has never been explored in detail.

Contemporary with early echinoids are another, now extinct, group of echinoderms with a complex jaw apparatus, the ophiocistioids. Although the jaw apparatus of ophiocistioids and echinoids were initially thought to be convergent (Haude and Langenstrassen 1976), it is now generally believed that the close similarity of lantern design in the two groups indicates homology and derivation from a common ancestor (Smith 1984). Like echinoids, ophiocistioids have five teeth braced within hemipyramids, but these teeth are of rather different appearance. These V-shaped elements have been described in detail by Haude and Langenstrassen (1976) and Piotrowski (1983).

Recently, new collections of well-preserved teeth of both echinoids and ophiocistioids have been made from the Late Ordovician and Silurian of Balto-Scandinavia (Kutscher and Reich 2004; Reich and Kutscher 2001). This material is well preserved and provides important new information on the detailed microstructure of teeth of primitive echinoids and ophiocistioids, which we document here. These data not only provide a firm basis for understanding how the modern tooth design evolved, but also shed light on the homology of this structure to the oral elements in other echinoderm groups.

MORPHOLOGY OF CROWN GROUP ECHINOID TEETH

All teeth of crown group echinoids are built along a similar plan, but with some variation in the size and shape of secondary tooth plates. The tooth is composed of three structural regions, the primary plate zone, the secondary plate zone and the stone zone (Text-fig. 1H), each structurally and functionally distinct (Wang et al. 1997). The tooth grows continuously from its aboral end (plumula) where new plates are added, and continuously sheds plates from the mature chewing edge. The primary plate zone forms the abaxial portion of the tooth and comprises a double stack of thin calcite sheets (primary plates) lying parallel to one another and packed closely together, but set oblique to the long axis of the tooth and inclined axially. The two series of plates overlap along the midline, and successive plates in the stack become welded together in the more mature part of the tooth by the growth of discs. A thin organic matrix fills the remainder of the space (Märkel et al. 1977). Primary plates have an amorphous core and crystalline rim (Wang et al. 1997).

Secondary plates form the axial portion of the tooth and develop as outgrowths from the lateral edges of the primary plates. Like the primary plates, these are vertically stacked, set oblique to the long axis of the tooth and are axially inclined. Their median edge is free. Secondary plates of grooved teeth are small simple elements, without projections, but they are large and triangular in the wedge-shaped teeth of irregular echinoids. In keeled teeth, the free end of the secondary plate gives rise to a long lappet-like structure (the carinal appendage), which forms the outer part of the projecting keel (Text-fig. 1C, F). As with primary plates, the secondary plates in the mature part of the tooth are bound together by calcite discs. The primary and secondary plates combined form a cone-in-cone stacked structure (Text-fig. 1).

The core of the tooth forms the cutting edge and is biomechanically the hardest zone of the tooth (Märkel and Gorny 1973). This so-called stone zone is constructed from a dense meshwork of prisms that grow from the adoral edge of the primary plates. These fibres extend aborally and are each surrounded by a thin organic matrix. Fibres are bound together and encased within a polycrystalline matrix of magnesium calcite. These fibres also extend along the core of the keel in keeled teeth, where they attain a much larger diameter. Probably, because of the high magnesium content of the calcite in the core of the stone zone, this is the hardest wearing part of the tooth. Wang et al. (1997) provided a detailed analysis and description of this part of the tooth.

The cone-in-cone structure of the primary and secondary plates, together with the extreme hardness of the stone zone, acts biomechanically to make the echinoid tooth self-sharpening. Plate-disc interfaces and fibre-disc interfaces are relatively weak and so allow cracks to propagate along the boundaries between plates. By contrast, the median part of the stone zone is much harder wearing and resembles a synthetic fibre-reinforced matrix composite in structure, which prevents large cracks from propagating in this region. As the core wears down as a result of abrasion, the abaxial primary and axial secondary plates, which are angled to form a cone around the core of the tooth, shear off. In this way, the tooth retains a natural sharp edge as it wears down (see Wang et al. 1997). Furthermore, the abaxial zone of primary plates is

arranged in such a way as to resist compressional stress, while the T-shaped cross-section of keeled teeth also reinforces the teeth against bending stress.

There is one more zone of stereom specialization. Along the sides of the abaxial surface is a single perforate stereom layer for insertion of the mutable connective tissue that binds the tooth firmly onto the hemipyramids.

Clearly, the teeth of modern echinoids are highly sophisticated structures that are incredibly well adapted for purpose. Crown group echinoids arose shortly before the end of the Palaeozoic (Smith et al. 2006) and by the late Permian echinoid tooth structure was essentially the same as that seen in modern echinoids (Smith and Hollingworth 1990). So, when and how did such a well-adapted structure arise? To answer these questions, we now turn to examine the structure of Lower Palaeozoic echinoid teeth from the Silurian of Gotland.

MATERIALS AND METHODS

Most of the material on which this study is based was collected during field work on Gotland, Sweden, over the last 10 years by Kutscher and Reich. Several hundred marl and rock samples (c. 500 kg) from more than 20 different localities (Text-fig. 2) were investigated using micropalaeontological techniques (Wissing and Herrig 1999). More than 100,000 echinoderm ossicles were isolated, including c. 5000 echinoid remains. Museum material from the Silurian of Gotland (21 further localities), collected by Anders Martinsson, Lars Ramsköld, Stefan Bengtson and Christina Franzen, housed in the Swedish Museum of Natural History in Stockholm, was also studied by one of the authors (MR). Finally, some Late Ordovician local glacial erratic boulder material collected on Gotland, Sweden, by Schallreuter and Reich is also included. In total,

TEXT-FIG. 2. Geological map of the Island of Gotland, Sweden showing the investigated localities that have yielded echinoid remains (modified from Calner et al. 2004a). Localities numbered as follows: 1, Nyhamn; 2, Häftingsklint; 3, Ygne; 4, Ireviken; 5, Snäckgårdsbaden; 6, Höglint; 7, Stajnkrogen; 8, Brissund; 9, Follingbo; 10, Robbjärn; 11, Sigfride; 12, Valbytte; 13, Halltega; 14, Tjelders; 15, Kvarnberget; 16, Solklint; 17, Tjeldersholm; 18, Smojge/Lilla Karlsö; 19, Lilla Karlsö; 20, Trädgården; 21, Hunnige; 22, Gannor; 23, Måstermyr; 24, Lau Backar; 25, Kättelviken and Husryggen; 26, Petsarve; 27, Hoburgen; 28, Uddvide.
almost 150 echinoid teeth and >500 ophiocistioid goniodonts from nearly all Silurian strata (Llandovery, Wenlock, Ludlow) exposed on Gotland were studied. The sedimentation in the Gotland area during Silurian times was dominated by carbonate deposition and reef formation in a shallow epi-continental sea at low latitudes (Laufeld and Basett 1981). The Silurian strata on Gotland are c. 500 m thick and range in age from Telychian (late Llandovery) to late Ludfordian (Ludlow). These deposits were subdivided by Hede (1921, 1960) into a series of stratigraphical units based on lithology and fossil content. More recently, study on the geology and stratigraphy of Gotland has been carried out by Calner et al. (2004a, 2004b), Jeppsson et al. (2006) and Jeppsson (2005, 2008). Detailed data on the mentioned localities can be found in Laufeld (1974) and Larsson (1979).

Specimens from the Öjlemyr flint were mostly collected in the north-western part of Gotland and are Ashgill (upper Pirgu stage) in age (Schallreuter 1981; Grahn 1982). Only the silicified parts in limestones and/or concretions were transported as local glacial erratic boulders (geschiebe), probably during Weichselian times from a region situated north-east of Gotland (Martinsson 1958; Eiserhardt 1992). The Öjlemyr flints are renowned for yielding a rich, diverse and well-preserved fauna (e.g. Schallreuter 1982; Reich 2001).

RESULTS

We recognize eight different kinds of tooth based upon differences in their microstructural organization. Each is described and illustrated below, and their stratigraphic distribution is summarized in Text-figure 3. For those elements found in the Silurian of Gotland, the associated echinoid plates are listed.

The material figured and mentioned herein is deposited in the collections of the Geosciences Centre of Göttingen University (GZG) and the Natural History Museum London (BMNH).

Simple oligolamellar teeth

Description. This type of tooth has a flat adaxial face and a weakly domed abaxial face with a shallow median depression (Text-fig. 4). For much of its length, it has parallel sides, but adorally it tapers to a relatively sharp point, the two sides converging at an angle of about 30–40 degrees. The tooth is constructed of a biseries of rectangular blocks (primary plates) angled at about 40 degrees to each other, alternating left and right and converging adorally. These blocks are about 1500 µm in length, 200 µm deep and 150 µm wide (Text-fig. 5A). The two series of elements abut along the midline where they overlap, slightly creating a zigzagged suture. In cross-section, there are three or four such rods abreast in each series. Each primary plate tapers abaxially and develops a slight curvature, becoming concave on its median face and convex on its distal face. This concave portion is most clearly seen in exposed elements at the tooth tip (Text-fig. 4F). Elements are stacked tightly together without intervening space, and there is no sign of discs or prisms linking the elements. Nor is there any abaxial stereom covering these elements.

The microstructure of these tooth plates is extremely dense, probably imperforate. There is no evidence of a meshwork of stereom in any specimen even in cross-section, and the plate elements may therefore possibly be composed of amorphous or polycrystalline calcite (as in modern echinoids where imperforate stereom is deposited (Märkel 1969)). This simple tooth morphology corresponds to the teeth described by Jesionek-Szymańska (1979, 1982) as smooth-edged oligolamellar, and by Prokop (1996) and Boczarowski (2001) as oligolamellar.
TEXT-FIG. 4. Scanning electron micrographs of simple oligolamellar teeth. A, adaxial view of tooth; GZG.INV.20093. B, adaxial view of tooth; GZG.INV.20096. C, abaxial view of tooth; GZG.INV.20094. D, cross-section through tooth, abaxial surface to top; GZG.INV.20034. E, detail of median part of tooth in adaxial view; GZG.INV.20096. F, tip of tooth in abaxial view; GZG.INV.20058. Specimens GZG.INV.20034, 20093, 20094, 20096 are from Lau Backar, Gotland (Eke Fm.; Ludlow: Ludfordian); GZG.INV.20058 is from Brissund (Högklint Fm.; Wenlock: Sheinwoodian). Scale bars represent 100 μm, except for E, in which it represents 20 μm.
Material. 52 specimens.

General occurrence. Wenlock to Middle Devonian (Givetian).

Occurrence on Gotland. Wenlock (Sheinwoodian) to Ludlow (Ludfordian).

Formations and locations on Gotland. Upper Visby Formation (Fm.) (at Snäckgårdsbaden), Högklint Fm. (at Bissund), Slite Group (at Solklint), Halla Fm. (at Smoige/Lilla Karlsö), Klinteborg Fm. (at Lilla Karlsö), Hemse Group (at Gannor), Eke Fm. (at Lau Backar), Burgsvik Fm. (at Kärne) and Hamra Fm. (at Hoburgen and Juves).

Associated echinoid plates. Aptilechinus, Bothriocidaris (only at Gannor), Neobothriocidaris and a possible new genus.

Rimmed oligolamellar teeth

Description. These resemble the simple oligolamellar teeth described previously in both overall appearance and construction.
They are composed of a biseries of block-like primary plates identical in shape and arrangement to those in simple oligolamellar teeth, but they are bounded laterally by an ancillary series of much shorter secondary blocks, running in parallel to the primary blocks but slightly offset (Text-fig. 5B). In the other, the adaxial face of primary and secondary tooth plates is sculpted with low sinuous ridges, and the outer edge of the tooth bears a row of short lateral denticles that curve adorally (Text-fig. 6A–B).

There are two distinct tooth morphologies with this structure. One has completely smooth primary plates and lacks lateral denticles (Text-fig. 5B). In the other, the adaxial face of primary and secondary tooth plates is sculpted with low sinuous ridges, and the outer edge of the tooth bears a row of short lateral denticles (Text-fig. 6A–B). Again the primary and secondary blocks abut tightly, and there are no discs or fibres binding the plates together.

Material. Two specimens.

General occurrence. Silurian (Wenlock to Ludlow).

Occurrence on Gotland. Wenlock (Sheinwoodian) to Ludlow (Ludfordian).

Formations and locations on Gotland. Upper Visby Fm. (at Ireviken) and Hamra Fm. (at Hoburgen).

Associated echinoid plates. Aptilechinus, Bothriocidaris (only at Gannor), Neobothriocidaris, Silurocidaris (only at Hoburgen) and a possible new genus.

Compound oligolamellar teeth

Description. These (Text-fig. 6C–D) have a flat adaxial and weakly domed abaxial surface and taper to a point adorally, as do all oligolamellar teeth. They differ in being constructed from multiple series of V-shaped plates. The central zone is composed of an alternating biseries of primary block-like plates, as in other oligolamellar teeth. These diverge from one another at an angle of about 35 degrees. After a short distance, they bend back sharply to form a V-shaped plate. A second V-shaped element follows laterally, slightly offset from the inner V-shaped plate. In large teeth, there may be another sharp bend in this outer tooth element, giving rise to a tertiary portion running parallel to the primary tooth plate. The two stacks of V-shaped elements are clearly separated from each other by a vertical suture, dividing the tooth into four discrete zones.

Material. 52 specimens.

General occurrence. Silurian (Wenlock to Ludlow).

Occurrence on Gotland. Wenlock (Sheinwoodian) to Ludlow (Ludfordian).

Simple lamellar teeth

Description. Teeth are concave adaxially and convex abaxially with a broad, raised median zone flanked by shallow grooves (Text-figs 7–8). Adorally the tooth ends in a single sharp point with rounded incisions on either side. The central zone is composed of steeply inclined primary tooth plates c. 50 µm apart. The space between primary plates is filled with pillars and stereo infill. At their outer edge, these primary plates start to merge with their neighbours, so that one in every three or four of the plates eventually continues as a large plate that first flattens out and then recurses. These secondary plates are about 100–150 µm apart in cross-section with dense calcitic spongy infill, without obvious structure. On the adaxial surface, the secondary plates form the entire face and are angle at about 60–70 degrees. Individual plates are separated by a stereom meshwork about 300 µm wide. The lateral zones are distinctly different and appear to be made up of longitudinally oriented and Anastomosing fibres. The primary and secondary plates thus form a nested series of loops. On the abaxial surface, the outer part of the secondary plates is covered by a thin layer of open stereom with a mean pore diameter of c. 8–10 µm, which continues to the outer edge.

This morphology corresponds to that of serrated teeth described by Boczarowski (2001, fig. 34B–C) as Albertechinus devonicus sp. nov.

Material. 87 specimens.

General occurrence. Silurian (Llandovery) to Late Carboniferous.

Occurrence on Gotland. Llandovery (Telychian) to Ludlow (Ludfordian).

Formations and locations on Gotland. Lower Visby Fm. (at Nyhamn), Upper Visby Fm. (at Häftingsklint, Ynge, Ireviken and Snäckgårdshad), Högklint Fm. (at Högklint and Stajnkrogen), Slite Group (at Pollingbo, Kalligate, Kvarnberget, Robbjäns, Sigfride, Solklint, Tjelders, Tjeldersholm and Valbytte), Halle Fm. (at Smoige/Lilla Karlso and Trädgården), Klinteberg Fm (at Hunnige), Hemse Group (at Gannor), Eke Fm. (at Lau Backar), Burgsvik Fm. (at Husryggen) and Hamra Fm. (at Hoburgen and Uddvide).
Associated echinoid plates. *Aptilechinus*, *Bothriocidaris* (only at Gannor), *Neobothriocidaris*, *Silurocidaris* (only at Hoburgen) and a possible new genus.

**Compound lamellar teeth**

*Description.* Like lamellar teeth, these are concave adaxially and convex abaxially with a broad, raised median zone flanked by shallow grooves (Text-fig. 9). However, adorally the tooth ends at a primary point flanked by two or more secondary points. In cross-section, the densely packed primary plates are separated by thin discs, and there is a median zone composed of vertical fibres that forms the abaxial face. Secondary plates are fewer than primary plates and are recurved. Successive plates are connected by short calcite discs. On either side of this central zone lie secondary series of primary and secondary tooth plates forming the core to the lateral tooth points. The abaxial face has a thin layer of perforate stereom forming outer lateral zones.

*Material.* Five specimens.

*General occurrence.* Early Carboniferous to Early Permian.

*Occurrence.* Tournasian, Lower Carboniferous, Tournai, Belgium.

*Associated echinoid plates.* *Archaeocidaris*.

Rogeriserra tooth elements

*Description.* These simple teeth (Text-fig. 10) have at their core a solid calcite rod, 1.0 mm long by 0.1 mm wide, and slightly...
flattened without obvious stereom structure. This rod is divided into an adoral head and a distal shaft. The head is flattened and multi-toothed and, like the shaft, is composed of solid calcite. There is a single median tooth and a short series of lateral teeth that originate alternately from left and right. The shaft is flanked by a single perforate stereom layer slightly less than 100 μm wide and edged by a solid rim. Pores in this zone are about 6–10 μm wide. The perforate stereom layer continues around the distal end of the tooth connecting the two flanking zones.

**Material.** More than 30 specimens.

**General occurrence.** Late Ordovician (Ashgillian).

**Occurrence on Gotland.** Ashgillian (Pirgu Stage).

**Formation and location.** Öjlemyr flint, local glacial erratic boulders from Gotland (origin north of Gotland).

**Associated echinoid plate.** Bothriocidaris.

**Linguaserra** tooth elements

**Description.** These (Text-fig. 11) are intermediate in form between Rogerserra-type mouth spines and true goniodont elements. They consist of a short blade-like element that has a proximal pointed head of solid calcite bearing a median tooth and many lateral denticles. Its distal half is composed of an open stereom mesh. One face is convex, the other concave, and, according to Boczarowski (2001), up to three elements are united to form a tooth battery.

**Material.** Three specimens.

**General occurrence.** Early Silurian (Llandovery) to Late Permian (Lopingian: Wuchiapingian) of Europe (Reich 2007).

**Occurrence on Gotland.** Llandovery (Telychian).

**Formation and location on Gotland.** Lower Visby Fm. (at Nyhamn).

**Sollasina-type goniodonts**

**Description.** These (Text-fig. 12) are compound structures made of a uniserial stack of V-shaped plates that become progressively smaller aborally. An individual plate is up to 2 mm in width with a primary central tooth and up to 12 slightly smaller lateral teeth distributed along the adoral edge. These teeth are composed of a core of very dense stereom with minute pores less than 1 μm wide, covered with a solid calcite crust. On one face (?abaxial) a smooth, imperforate calcite zone forms the proximal half of the tooth plate, while the distal half is slightly angled and thins aborally. This aboral zone is composed of a regular open mesh stereom with a pore diameter of around 5–8 μm. On the other face (?axial), the zone immediately behind the teeth is concave and ridged, the intervening indentations matching in shape and size to the individual denticles. Aboral to this ridged and pitted zone comes a zone of open stereom with pores similar to those on the abaxial side.

**Material.** More than 500 specimens.

**General occurrence.** Late Silurian (Ludlow) of Sweden and the United Kingdom (Reich and Haude 2004).

**Occurrence on Gotland.** Ludlow (Ludfordian).

**Formation and location on Gotland.** Hemse Group (at Gannor and Måstermyr), Eke Fm. (at Mallgårdsklint, Petsarve and Russpark), Burgsvik Fm. (at Kåttelviken), Hamra Fm. (at Hoburgen and Husrygg).

**DISCUSSION**

We have found that a range of different tooth morphologies existed in the Silurian. These are all simpler in structure than the teeth of crown group echinoids, including the teeth of Permian miocidarids described by Smith and Hollingworth (1990). Some of these morphologies have been described previously in the pioneering studies of Jesionek-Szyman’ska (1979, 1982). In those papers, she recognized and described simple oligolamellar teeth and also distinguished a second form of tooth that corresponds to our rimmed oligiolamellar teeth. Unlike our simple oligolamellar teeth, which have 3–4 primary elements abreast, her Devonian oligolamellar teeth differ in having 6–8 primary elements abreast in each half series. She also provided illustrations of lamellar teeth but never described these in detail.

All the materials described here and that described by Jesionek-Szyman’ska are of isolated teeth collected from...
sieved sediment samples. Consequently, it is not possible to say with certainty to which taxonomic group each form belongs. We therefore surveyed partial and complete test material in museum collections as well as those described in the literature to record associated tooth structure.

Simple oligolamellar teeth occur in the Upper Ordovician *Aulechinus*, the Silurian *Echinocystites* and the Early Devonian *Rhenechinus*. We have yet to identify any echinoid with rimmed or compound oligolamellar teeth. However, simple lamellar teeth are found in the Late Silurian *Palaeodiscus* (BMNH E34360) and the Carboniferous *Pholidechinus, Pholidocidaris* (BMNH E77751), *Melonechinus* (BMNH E82729) *Hyattechinus* (BMHN E12262) and *Lepidesthes* (BMNH E10699). Compound lamellar teeth are seen in Carboniferous *Archaeocidaris* and possibly also in *Meekechinus* (cf. Bindemann 1938). *Rogeriserra* and *Linguserra* have not been observed in any articulated specimen, and it is not certain from which major taxonomic group they come from. The close similarity between *Linguserra*-type elements and goniodonts, however, suggests ophiocistioid affinities. *Sollasina*-type goniodonts are seen in the ophiocistioids *Sollasina, Eucladia, Rotasaccus* and *Gillo-cystis*.

Understanding the structure of these earliest teeth is important for two reasons: it helps us understand how teeth may have arisen in the first place, and it provides insight into the early biomechanical evolution of this most specialized and highly adapted skeletal element.

**TEXT-FIG. 11.** Drawing of the holotype tooth of *Linguserra ligula* Langer, 1991, from an original SEM. micrograph. Givetian, Middle Devonian. Daasberg near Gerolstein, Rhineland-Palatinate, Germany.

**Origins of echinoderm teeth**

The lanterns of ophiocistioids and echinoids are very similar indeed. Both are made up of five compound units each consisting of a large pair of hemipyramids sutured together along their interradial suture, an interradial tooth that rests on the inner surface of the pyramids, a pair of epiphyses fixed to the aboral end of the hemipyramids and a rotula articulated to epiphyses from adjacent pyramids. Muscle attachment sites on the hemipyramids show that the five pyramids are attached by protractor and retractor muscles to the corona and connected to each other by a large block of interpyramidal muscle. Despite the undeniable close homology of the ophiocistioid and echinoid lanterns, detailed comparison of tooth construction surprisingly implies that they may have arisen independently.

Whereas the echinoid tooth is composed of a stacked alternating biseries of inclined, rod-like elements, the ophiocistioid tooth comprises a stacked single series of blade or plate-like elements. *Rogeriserra* represents the most primitive tooth morphology that we have encountered, but unfortunately it remains known only from isolated tooth elements. Our reconstruction of the complete tooth battery is therefore based on functional analysis of these individual elements. Each individual element is very spine-like with a reinforced core of solid calcite. The expanded and flattened denticulate head clearly forms the biting tip, while the flanking perforate stereom along the shaft presumably housed binding ligament that connected successive elements forming a cohesive battery of barbed teeth (Text-fig. 13A–B). As the perforate stereom zones are no wider than the biting tip (Text-fig. 10A), it seems unlikely that elements overlapped laterally and, in contrast to the situation in goniodonts, there is no evidence that the elements in *Rogeriserra* were offset one above the other, so the tooth battery was presumably a simple vertical stack of elements. Some tooth elements (e.g. Text-fig. 10C) are distinctly asymmetrical raising the possibility that there were left and right stacks in the tooth batteries of some taxa. Furthermore, both the primary plates of oligolamellar echinoid teeth and the central rod of *Rogeriserra* ophiocistioid teeth are composed of a dense calcite. Thus, the median rod in the *Rogeriserra*-type ophiocistioid tooth may be homologous with a single rod-like element in primitive oligolamellar echinoid teeth. If so, then the teeth of echinoids and ophiocistioids share homology only at a very basic level and presumably have evolved independently from simple rod-like mouth spines. The biserial alternating plate organization of echinoid teeth and the multiple battery organization of ophiocistioid teeth are independent solutions to maintaining a sharp biting surface, as discussed later.
The only other group of echinoderms to possess a muscular jaw apparatus is the ophiuroids, and drawing comparisons with this group provides insight into how the more advanced teeth of echinoids and ophiocistioids arose. The jaw of early Palaeozoic ophiuroids is simpler in structure being composed of five V-shaped jaws, each constructed of two pairs of ambulacral plates (Shackleton 2005; Text-fig. 13C). The first pair (or mouth angle plates) meets interradially and are bound together by ligamentary tissue (like the hemipyramids of echinoids and presumably ophiocistioids). The second ambulacral ossicles are bound by ligaments to the mouth angle plates and are presumably homologous with the epiphyses. There is a vertical series of oral spines that are attached to the proximal end of the mouth angle plates and which project into the mouth opening. These spines are usually oral-aborally flattened, short and squat with a broad inner edge, and are usually stacked vertically as a single column, although the outermost can often be paired. Muscles attach to the two V-shaped wings of the jaw in modern ophiuroids and are used in closing and opening the mouth.

Thus, the Rogeriserra-type rod the primary plates of echinoid oligolamellar teeth, and the individual V-shaped goniodont elements are all probably homologous with ophiuroid mouth spines. In all cases, these tooth elements lie adaxial to the first ambulacral plates (hemipyramids), are arranged in vertically stacked series and are bound to hemipyramids. We propose that in echinoids, the tooth arose from paired mouth spines that became angled and intimately bound together to form a single cohesive structure, the oligolamellar tooth. The teeth of ophiocistioids on the other hand must have evolved from a uniserial arrangement of stacked tooth spines, with the mouth spines remaining horizontal and becoming tightly bound together with interconnecting ligaments.

Biomechanical evolution of teeth

Modern echinoid teeth need to be sharp, strong and resilient, especially to bending and compressional stresses. They achieve this by a combination of growth and

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structural design adaptations, which make the teeth self-sharpening, as described previously. The Silurian teeth are much less specialized and provide key evidence for when and how such specialization arose.

Continuous growth and replacement. No modern ophiuroid shows continuous mouth spine replacement, although presumably lost or broken mouth spines can be repaired or replaced in the same way as any echinoderm spine (e.g., Dubois and Ameye 1995). A major advance in biomechanical design came therefore with the evolution of a continuous conveyor belt production of tooth plates or their antecedent mouth spines. In echinoids, new plates are continuously added at the aboral end of the tooth to replace elements at the adoral tip as it is worn down. The tooth therefore has to shift adorally as it grows, and this creates conflict with the need to have the tooth firmly bound to the hemipyramids (Birenheide et al. 1996). Continuous growth and replacement was clearly in place even in the earliest of echinoid teeth. However, it was not until the evolution of lamellar teeth that we see the first evidence for specialized zones of stereom where binding ligament would have connected the tooth to the hemipyramids. The organization of ophiocistioid teeth, whereby progressively smaller goniodont elements are stacked above one another, also strongly implies that they grew in a conveyor belt-like manner, with continuous replacement taking place as adoral elements wore down.

As both echinoids and ophiocistioids appear to have evolved a strategy of continuous growth and replacement of tooth elements, it is tempting to assume that such a strategy was already established in their latest common ancestor. However, there is no evidence for continuous replacement of Rogeriserra-type elements. Either Rogeriserra-type elements come from stem group (echinoids + ophiocistioids), or both clades independently evolved the same strategy.

Self-sharpening mechanism. Because ophiuroid mouth spines are not continuously replaced, they have no mechanism for self-sharpening. There is also no evidence of self-sharpening ability in Rogeriserra-type elements, which were probably no more than a vertical stack of spines bound together with interconnecting ligament. However, self-sharpening is a common feature of the other teeth described here.

Ophiocistioid goniodont elements are arranged as an offset stack of elements in which only the lowest, most adoral, forms the actual biting surface. The abaxial zone of open stereom on axial and abaxial surfaces we interpret as the insertion site for the ligament that bound together the successive goniodont elements. The stack of goniodont elements fit together very tightly, because the axial surface of one element is notched to accommodate contours of the next goniodont element. In this way, the successive elements all interlock and reinforce one another against compressive stress. This V-shaped battery of goniodont elements also provides a means of self-sharpening; once the leading edge goniodont becomes damaged or worn down, the entire plate would simply shear off leaving the next goniodont in position. This presumably involved weakening and rupture of the binding ligament.

Self-sharpening in the echinoid teeth evolved to a much more advanced state, and even the most primitive forms show some ability towards self-sharpening. In simple oligolamellar teeth, the sharp biting point is formed of just the leading edge of a single tooth plate (Text-fig. 4F). These teeth were thus presumably able to maintain a sharp point by shearing off alternately left and right primary plates as the tip wore down. Thus, new tooth plates were constantly being exposed at the tip. However, because each individual plate is rather thick, the tooth had no means of developing a sharp cutting edge along the axial–abaxial plane.

A sharper cutting edge was achieved, however, with the development of thinner, buttressed primary plates with secondary flanges. In such teeth, the individual tooth plates are narrow, curved and supported by wide flanges, and so the biting point can be much narrower (Text-fig. 7D). In large teeth, multiple sharp points were developed (Text-fig. 9B), by the simple expedient of having multiple columns of stacked tooth plates. However, broad abaxial primary plates that have secondary plates developed on their axial face had not yet evolved. This organization is first seen in the Permian miocidarids (Smith and Hollingworth 1990), and with the evolution of this cone-in-cone arrangement of plates teeth could, for the first time, become self-sharpening in both the axial–abaxial and the medial–lateral axis.

Hardening of biting surface. The biting tip of teeth needs to be hard and resistant to compressive stresses. Ophiuroid mouth spines are constructed from a standard stereom meshwork and are undifferentiated from the other spines that cover the body. Furthermore, they remain unconnected to their neighbours and thus act independently. In echinoids and ophiocistioids, the tooth elements are physically bound together to provide a reinforced tooth. Even in the most primitive Rogeriserra-type elements, the individual elements must have been bound together to form a single vertical battery of points. In addition, both ophiocistioid and oligolamellar tooth plates have a very different microstructure, being composed of what appears to be finely granular and imperforate calcite. This creates a denser and stronger structure. In modern teeth, the strength of critical parts of skeletal elements is also increased by the addition of magnesium, but it is not known whether this is true also of these early teeth.
The strength of calcite elements can be increased only so far by making them physically denser. Ophiocistioid tooth elements did not evolve beyond this stage, and even the most advanced goniodonts simply have a marginal band of imperforate stereom from which the denticles arise (Text-fig. 12C–F). In the oligolamellar teeth of echinoids, individual tooth plates were also initially thick and composed of very dense calcite. However, an important advance came with the evolution of the lamellar tooth. Lamellar teeth have a structure of thin plates buttressed by numerous short pillars. The advantage of this is that it creates a lighter structure better able to cope with compressional stress and more resistant to crack propagation. Furthermore, by the Carboniferous a system of fibres, initiated along the leading edge of primary tooth plates and extending along the axis of the tooth, had evolved. These fibres are welded together by amorphous calcite creating a composite core to the tooth. This composite structure resembles the arrangement seen today in the core of echinoid teeth and which provides this zone with such great strength and resilience (Wang et al. 1997). However, it was not until the Permian miocidarid crown group echinoids that we see these fibres extending between the primary tooth plates to form a more extensive reinforced zone (Smith and Hollingworth 1990).

The detailed similarity of ophiocistioid and echinoid lanterns is striking, but it is evident from our detailed analysis that their teeth are only homologous at a very basic level. Furthermore, both appear to have evolved their own particular self-sharpening mechanisms. At present, we do not know what sort of echinoderm Rogeriserra elements belong to (although their association with Bothriocidaris elements is suggestive). As this form of tooth seems to bridge the gap between ophiuroid mouth spines and the more sophisticated tooth plate batteries of echinoids and ophiocistioids, it would be of great interest to discover these elements in situ. Placing this tooth structure more securely within a phylogeny of echinoderms would help to determine whether processes such as tip-hardening through the evolution of denser calcite and the continuous replacement mechanism were evolved once in the common ancestor of echinoids and ophiocistioids, or represent further examples of biomechanical convergence.

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