Translating taxonomy into the evolution of conodont feeding ecology

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ABSTRACT

Conodont research has long been divided between utilitarian applications to solve geological problems versus analysis of their paleobiology. However, recent advances in conodont functional analysis allow these independent stands of research to be unified, decoding the functional implications of their morphological variation. We demonstrate this using synchrotron tomography and finite element analysis, informed by occlusal and microwear analyses, to analyze functionally the classic evolutionary sequence of the genus *Polygnathus*. Our study shows that the evolution of the platform in *Polygnathus* occurred to accommodate and dissipate the stress accumulation derived from the tooth-like function that the P_1 elements performed, suggesting that this recurrent motif of conodont evolution represents an adaptive response to recurrent functional selective pressures. Our study establishes a framework in which the functional ecology of conodonts can be read from their rich taxonomy and phylogeny, representing an important attempt to understand the role of this abundant and diverse clade in the Phanerozoic marine ecosystems.

INTRODUCTION

Conodonts are major components of Phanerozoic marine ecosystems; they have a wide geographical and temporal distribution, and are characterized by rapid morphological evolution through their long stratigraphic ranges, from late Cambrian to end-Triassic. Since their discovery, the history of conodont research has been split between their applications to solve utilitarian geological problems versus their paleobiology. Conodont biozones and the taxonomy on which they are built have long been applied to resolve regional and intercontinental-scale correlations. Conodont paleobiology has been dedicated to elucidating their biological affinity and the function of their mineralized skeleton. The development of methods for functional analysis of conodont elements has now progressed to stage where these disparate strands of conodont research may be unified. Microwear analysis, computed tomography, and finite element analysis can now be combined to interpret conodont taxonomy, stratigraphy, and phylogeny in terms of feeding ecology (Jones et al., 2012; Martínez-Pérez et al., 2014a). We demonstrate this through the functional analysis of the classic phylogeny of *Polygnathus* species, one of the most prolific of all conodont evolutionary lineages (Becker, 2012), by means of occlusion, microwear, and finite element analyses. Our study is focused on the morphological evolution of the earliest species in which its characteristic dorsal platform developed from a blade-like ancestral morphology. This transformation is a recurring evolutionary pattern in conodonts (Sweet, 1988) for which our study seeks a general interpretation, attempting to elucidate the role of this abundant and diverse clade in Phanerozoic marine ecosystems.

BRIEF HISTORY OF *POLYGNATHUS* RESEARCH

Polygnathus species have been studied intensively for taxonomy, phylogeny, and biostratigraphy based on the morphological evolution of their P_1 elements (Becker, 2012) (Fig. 1A). *Polygnathus* evolved during the
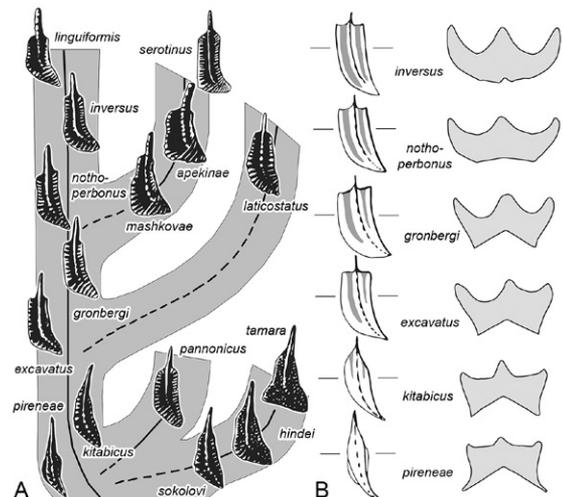
Figure 1. Early evolution of *Polygnathus*. A: Proposed phylogenetic relationships among the early species of the genus. B: Principal morphological trends: left side illustrates the upper morphological characteristics and right side shows median cross sections. Modified from Yolkin et al. (1994).

Pragian, and is characterized by the development of a dorsal platform from its ancestral blade-like condition in the P_1 element position (Mawson, 1998). The phylogeny of early polygnathids is among the most extensively studied and, based on coeval sections worldwide, is hypothesized to have evolved from the *Eognathodus* group (Mawson, 1995, 1998; Bardashev et al., 2002). *Polygnathus* underwent a dramatic diversification in the Emsian, characterized by increasing the platform size, changes in the oral surface of the platform, and the inversion of the basal cavity (Yolkin et al., 1994). More than 650 species have been attributed to the genus, evidencing their significance in Devonian and Carboniferous marine ecosystems (Becker, 2012). However, the functional morphology of *Polygnathus* P_1 elements is poorly understood, and few studies have attempted to resolve their function within the apparatus (Nicoll, 1987). We sought to interpret the functional morphology of *Polygnathus* P_1 elements based on specimens from natural assemblages, representing the skeleton of single individuals, and thus containing elements that functioned together in life.

MATERIAL AND METHODS

Our research comprised two principal analyses: (1) occlusal and microwear analyses to develop the functional model for the genus, and (2) finite element analysis of different species of the genus informed by the occlusal and microwear analyses previously performed. Our functional model is based on analysis of articulated clusters and disarticulated P_1 elements of *Polygnathus xylus xylus* from the upper Devonian of the Canning Basin, Western Australia (Nicoll, 1985). Clusters including pairs of P_1 elements were characterized using synchrotron radiation X-ray tomography (SRXTM) at the TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institute (Villigen, Switzerland). Three-dimensional (3-D) virtual

models were extracted using AVIZO v.7.1, from which enlarged physical models (×150) were created using a Makerbot Replicator 2 printer. These physical models were used to inform our digital occlusal analysis with Geomagic Studio v. 12 (www.geomagic.com). The occlusal model was corroborated with microwear data from isolated P_1 elements of *P. xylus* from elements associated with the clusters. All specimens are reposited at the Commonwealth Palaeontological Collection (Canberra, Australia).

We used the occlusal and microwear results to inform the position of our 2-D finite element analysis, a conventional engineering technique used to analyze the stress and strain within biologically complex shapes. The occlusal and wear analyses showed that the most constrained region of the platforms coincides with the cross sections of adult forms that have been used to characterize the early evolution of *Polygnathus* through the Pragian–Emsian, i.e., *P. pireneae*, *P. kitabicus*, *P. excavatus*, *P. gronbergi*, *P. nothoperbonus*, and *P. inversus* (Yolkin et al., 1994, their figure 2) (Fig. 1B). Those cross-section models were used to develop our 2-D finite element analysis to simulate the occlusion process with the software COSMOSM (SRAC, Structural Research and Analysis Corporation, Santa Monica, California). Model comparison was facilitated by equal force per surface area scaling (Table DR1 in the GSA Data Repository[1]), meaning that we applied a functional load proportional in magnitude to surface area, therefore removing the effects of model size and providing a comparison of stress-strength performance based solely on shape (Dumont et al., 2009). Because we used a linear elastic model of a slice of conodont crown, the magnitude of the applied load does not affect the pattern of stress distribution. We did not attempt to infer absolute stress or strain magnitudes, only relative magnitudes and stress distribution imposed by simple occlusal loads. (For a detailed description of the methods, see the Data Repository.)

RESULTS

Polygnathus Morphology

Polygnathus P_1 platforms show an extremely conservative morphology, making the genus easily discernible from other conodont taxa. P_1 elements are characterized by a ventral free blade and a rostrally and caudally expanded dorsal platform (Fig. 2A). The free blade is ornamented with sharp laterally compressed denticles, while platforms are usually ornamented with small ridges or nodes and a central carina flanked by two adcarinal troughs. In aboral view, *Polygnathus* P_1 elements have a basal cavity that is broad and deep in the earliest polygnathids, but reduced in size through phylogeny.

Our occlusal analysis is based on a natural articulated pair of elements assigned to *P. xylus xylus* from the upper Devonian of Australia (Nicoll, 1985). Morphologically, *P. xylus xylus* exhibits the general features of the genus, allowing us to derive a general occlusal model for all *Polygnathus* species. In this sense, *P. xylus xylus* shows a free blade that composes half the length of the element, and with a lanceolate platform that is constrained laterally in the ventral region. The dorsal region of the platform is curved slightly toward the rostrum. The surface of the platform bears well-developed adcarinal troughs that reach the dorsal tip of the element, with the edges of the rostral and caudal platform ornamented by ridges in the ventral region, and more rounded denticles in the dorsal region. The basal cavity is completely inverted, with a single keel, and the basal pit is located in the ventral region of the platform.

Occlusal Analysis

We analyzed the pattern of occlusion in *P. xylus xylus* P_1 elements using virtual models derived from SRXTM characterization of the natural
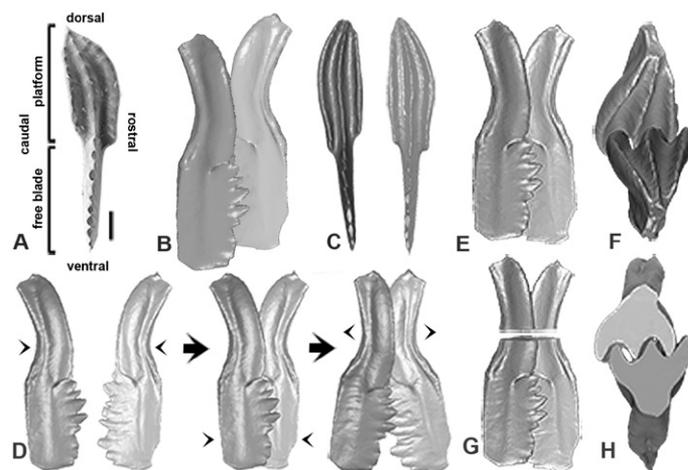
Figure 2. *Polygnathus xylus xylus* P_1 elements. A: Left P_1 element showing orientation and morphological terms (CPC42065; Commonwealth Palaeontological Collection, CPC, Canberra, Australia). Scale bar 100 µm. B–H: Tomographic models based on the cluster CPC25176. B: Cluster three-dimensional model. Scale bar 139 µm. C: Occlusal pair dissected in oral view. Scale bar 139 µm. D: Occlusal cycle in oral view. Not to scale. E–H: Most constrained stage of the cycle in oral (E) and dorsal (F) views. Not to scale. G, H: Detail in cross section showing the complete intermesh between opposite elements.

articulated element pair, and 3-D physical prints of these models. The physical models allowed us to explore the physical interaction of the elements, allowing us to establish a hypothesis of occlusion that we analyzed *in silico* and tested subsequently using microwear data. In their preserved state, this and other natural articulated element pairs (Nicoll, 1985, his figures 4C, 4F, and 4I) are preserved such that the oral surfaces of the left and right elements are intermeshed with the rostral side of the left element's blade overlapping with the caudal side of the right element's blade (Fig. 2B). Given that the elements are preserved in this occluded position in several clusters, we interpret this as reflecting an *in vivo* condition. Clusters of elements that are not preserved in this manner reflect post-mortem reorientation (Nicoll, 1985, his figures 4B, 4G, and 4H).

Based on analysis of the interaction between the scale-enlarged physical prints of the P_1 element pair and the occluded juxtaposition preserved in the natural articulated element clusters, we derived an hypothesis for their occlusal cycle (Fig. 2D). The oral faces of the element pair are brought together bilaterally, with the blade of the left element behind the right element, acting as guides and aligning the elements for the approach of the platforms during the occlusal cycle. In this position, the opposing elements interlock with great stability, the carina and the edge of the rostal platform of the left element interdigitate with the caudal and rostral troughs of the right element. This is the principal point of rotational articulation between the two opposite elements. As the process of platform occlusion proceeds about this point, the mid-dorsal regions of the platforms are brought into contact, still controlled by the interlocking carina and troughs of the opposing elements. However, the simpler oral surface ornamentation of this region of the platform, with shallow troughs and small ridges or rounded denticles, together with the loss of contact between the blades, implies a loss of blade control in the interaction when the dorsal portions of the platforms are in occlusion.

Occlusal analysis of the digital models confirms the inferences based on physical modeling and provides a more detailed insight into its occlusal morphology (Figs. 2E–2H). The principal point of articulation occurs at the ventral end of the caudal platform (Fig. 2E). Here, the more excavated adcarinal troughs and the more complex oral ornamentation constrain the relative motion of the two platforms (Fig. 2H). The occlusion process is less precise in the dorsal region of the platforms, where the shallower adcarinal troughs do no allow a clear interlock. These results suggest a model in
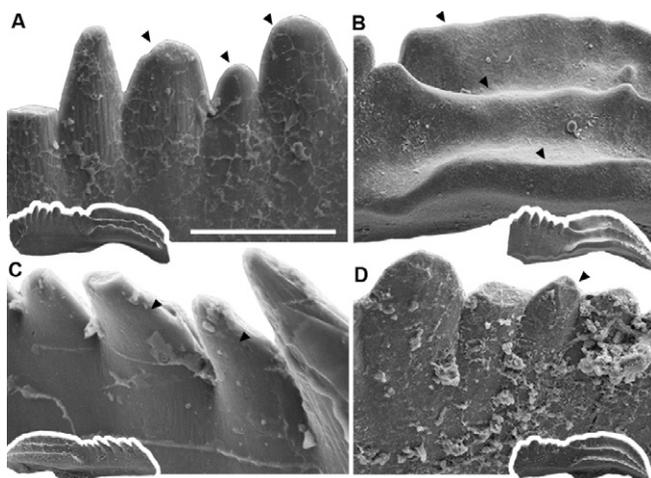
which the opposed P$_1$ elements of *Polygnathus* exhibit bilateral occlusion, with a short rotational movement from ventral to dorsal following element curvature. In this cycle, the principal point of articulation is located at the ventral end of the caudal platform, where the morphology of this area constrains the relative motion of elements and facilitates precise occlusion.

Microwear Analysis

Well-preserved P$_1$ elements of *P. xylus xylus* exhibit a striate surface micro-ornament on the blade denticles and a polygonal micro-ornament on the platform denticles. The elements show clear evidence of wear where the striate surface texture on the blade denticles was removed by smooth polishing on both sides of the blade's denticles (Figs. 3A and 3C), and the polygonal ornamentation was removed from ventral areas of the platform (Fig. 3B). In addition, there is evidence of mesowear, concentrated on the blade denticles tips and the central carina in the ventral area of the platform. The denticles of the blade have rounded tips, so worn in some specimens as to make adjacent denticles indistinct, instead forming a continuous and concave ridge in the area that joins the platform (Fig. 3B). Well-defined facets occur in the external edge of the caudal platform in right elements, and in the external edge of the rostral platform of left elements (Fig. 3B). In both instances, the long facets extend through to the middle of the platform but they do not reach the dorsal region. Spalls occur on both sides of the blade where sheets of crown tissue have been dislocated by brittle fracture, although they are low in number and concentrated on the ventral half of the element (Fig. 3D). No evidence of wear was found on the dorsal part of the platform.

Finite Element Analysis

Our 2-D finite element analysis was focused on the ventral region of the platform, following the results of our occlusal and wear analyses, which indicate that this region is most heavily constrained within the occlusal cycle (Fig. 2E). We derived six different finite element models, based on the classic evolutionary hypothesis proposed by Yolkin et al. (1994, their figure 2) that characterizes the early evolution of polygnathids in terms of the cross-sectional profile of the P$_1$ elements. All models were scaled to remove size differences, comparing directly in terms of their shape differences (Table DR1). The species are considered in the order of their position within the phylogeny of *Polygnathus* presented by Yolkin et al. (1994), from primitive to derived.
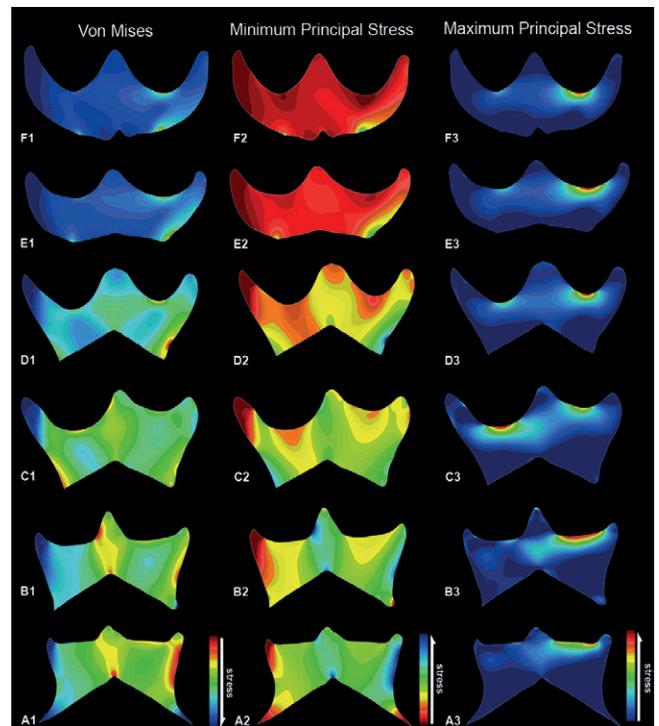
Von Mises, maximum, and minimum principal stresses results are shown in Figure 4. In *P. pireneae*, the Von Mises stress shows that the entire element is highly stressed, with high peaks in the central region, at the oral surface, and around the basal cavity (A1 in Fig. 4). This same general pattern is seen also in the compression stress plots (A2 in Fig. 4), while tensile stress is concentrated close to the oral region (A3 in Fig. 4). *P. kitabicus*, *P. excavatus*, and to a lesser extent *P. gronbergi* share broadly those patterns, with Von Mises stress focused in central areas of the platform but with clear differences compared to *P. pireneae*. In these three species, the stress is concentrated mainly in the central region of the platform (including the carina denticle), and at the oral surface beneath the adcarinal troughs, but with areas of low stress in the lateral regions of the platform (B–D, Fig. 4). This pattern is clearly visible in the compressive stress plots (B2, C2, and D2 in Fig. 4), where low levels of stress in the region beneath the adcarinal troughs increase incrementally through the phylogenetic sequence of species. Comparative tensile stress magnitude and distribution show little change compared with *P. pireneae* (B3, C3, and D3 in Fig. 4). In the most derived species, the P$_1$ elements of *P. nothoperbonus* and *P. inversus* exhibit the lowest concentration of stress, relative to less-derived species. The Von Mises stress is concentrated primarily in the surface of the elements, the upper areas of the platform, and the areas close to the edge of the basal cavity in the aboral region (E1 and F1 in Fig. 4), following the same general patterns as the principal minimum stress (compressive) (E2 and F2 in Fig. 4). Tensile stress is localized at the oral surface, focused in the adcarinal troughs (E3 and F3 in Fig. 4).

DISCUSSION

Occlusal Cycle of *Polygnathus* P$_1$ Elements

Our occlusal and wear analyses demonstrate that the opposed P$_1$ elements of *Polygnathus* exhibit a complex bilateral interpenetrative

Figure 3. Wear evidence on *Polygnathus xylus xylus* P$_1$ elements indicated by arrows. A: Smooth polishing of blade denticles (CPC42066; CPC—Commonwealth Palaeontological Collection, Canberra, Australia). Scale bar 50 μm. B: Smooth polishing of platform (CPC42067). Scale bar 200 μm. C: Smooth polishing of the striate ornamentation on the non-occlusal side of the blade (CPC42068). Scale bar 30 μm. D: Spalls on the occlusal side of the blade (CPC42069). Scale bar 100 μm.

Figure 4. Two-dimensional finite element analysis of several species of *Polygnathus* derived from the cross section of P$_1$ element platforms focused on the ventral domain of the platform, showing Von Mises (left), minimum (mainly compressive) (center), and maximum (mainly tensile) (right) principal stresses. A—*P. pireneae*. B—*P. kitabicus*. C—*P. excavatus*. D—*P. gronbergi*. E—*P. nothoperbonus*. F—*P. inversus*. Based on Yolkin et al. (1994, their figure 2).

occlusion. The ventral blades contact first, acting as guides, aligning the elements and facilitating the approach of the platforms during the occlusal cycle. The principal point of articulation occurs at the ventral end of the caudal platform, where the free blade joins the platform (Figs. 1A and 2E). Here, the adcarinal grooves, combined with a more complex morphology, constrain the relative motion of elements and facilitate a precise occlusion. In contrast, the occlusion is less precise in the dorsal region of the platforms where the adcarinal troughs became shallower, showing imprecise occlusion of the carina and troughs of the opposite elements. These results suggest a model in which the elements occluded in a short rotational movement from ventral to dorsal following the curvature of the oral surface of the element, stopping in the middle part of the platform, not contacting the most dorsal regions of the elements. This model is compatible with the general model originally described by Donoghue and Purnell (1999). This hypothesis is supported by the evidence of surface wear, which is concentrated in the ventral region of the platform, particularly along the denticles of the carina, and on the edges of the platform (Figs. 3A and 3B). In addition, the presence of spalls on the blade indicates that the elements were separated during the occlusal cycle to facilitate the entry of food materials for processing and, thus, sometimes maloccluded.

The occlusal cycle of *Polygnathus* is comparable to the rotation cycle described for *Gnathodus bilineatus* (Martínez-Pérez et al., 2014a) and *Wurmiella* (Jones et al., 2012), which also show evidence of episodic separation of the opposed elements as part of the occlusal cycle. This cycle is facilitated by the convex curvature of the oral surface of the platform, differing from the occlusal cycle of *Pseudofurnishius murcianus* P$_1$ elements where the straight blade required that the opposing elements approached orthogonally to the plane of attachment of the elements (Martínez-Pérez et al., 2014b).

Evolution of *Polygnathus* Function

The major morphological transformation of the P$_1$ element, from simple carminate blade to complex platform, characterizes the early evolution of species in the genus *Polygnathus* (Sweet, 1988). The increase in platform size occurred gradually, both through ontogeny and phylogeny, followed by more subtle changes in oral morphology and in the basal cavity configuration (Yolkin et al., 1994; Mawson, 1998). Our finite element analyses allowed us to interpret these morphological changes, suggesting that the development of the adcarinal troughs and the reduction (inversion) of the basal cavity reflects functional optimization to accommodate and dissipate functionally derived stress. In addition, adcarinal troughs and increased complexity of the ornamentation provided better occlusal control. These changes may evince a general evolutionary trend among species within the genus, to apply greater loads in the processing of food materials, and hence expanding the variety of food resources.

Iterative Evolution of Conodont Dental Morphology

Sweet (1988) identified the iterative phylogenetic transformation of P$_1$ elements, from blade-like to platform elements, as a recurrent theme in conodont evolutionary history, associated with the beginning of eustatic transgressive pulses, reaching peaks of diversity during transgressive highstands. It is likely that this pattern reflects some artifact of facies bias, yet the general pattern must be real because instances of platform evolution are demonstrably phylogenetically independent (Sweet, 1988). If the results of our analysis of *Polygnathus* may be generalized to the evolution of platform elements in other conodont lineages, they suggest that the iterative evolution of platform conodonts is associated with the accommodation of (presumably increasing) functional loads. This extended the range of food resources available, allowing species to explore the new available niches created during those transgressive pulses, and favoring the morphological specialization and diversification of conodont lineages.

CONCLUSIONS

Our integrated physical and computed functional analysis of an evolutionary series, *Polygnathus* P$_1$ elements, reveals that they interacted through precise bilateral occlusion developing an efficient tooth-like function. Finite element analysis indicates that the phylogenetic transformations of *Polygnathus* P$_1$ elements, from simple blades to platform elements, reflect adaptation to greater functional loads, dissipating the accumulation of implied stress. This may provide a more general explanation for the recurrent phylogenetic pattern of morphological transformation, from blade to platform elements, that characterizes the evolution of many conodont lineages. Our study foreshadows a reinterpretation of conodont taxonomy and systematics in terms of the evolution of feeding ecology and the contribution of this diverse clade of primitive vertebrate to Phanerozoic ecosystems.

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